FAUNAL DISTRIBUTION AND DEPOSITIONAL ENVIRONMENTS IN THE LOWER BRINGEWOODIAN (LUDLOVIAN) OF WALES AND THE WELSH BORDERS

by

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DECLARATION

The material presented in this thesis summarises the results of research carried out between July 1976 and July 1979 in the Department of Geology, University of Glasgow, under the supervision of Dr. J.D. Lawson. This dissertation is based on my own independent research and any published or unpublished material used by me has been given full acknowledgement in the text.

D.R. Atkins

August 1979

NOTE

During the preparation of this thesis, work by Cocks (1978) and Harper & Boucot (1978a, 1978b, 1978c) makes it necessary to add this note.

The following taxa referred to in this work : Amphistrophia funiculata (M'Coy), Craniops implicata (J. de C. Sowerby), Mesopholidostrophia cf. lepisma (J. de C. Sowerby), Shagamella ludloviensis Boucot & Harper, Shaleria sp. nov. and Strophonella euglypha (Dalman) should now, respectively, be referred to as: Amphistrophiella funiculata (M'Coy) (Harper & Boucot 1978b), Craniops implicatus (J. de C. Sowerby) (Cocks 1978), Pholidostrophia cf. lepisma (J. de C. Sowerby) (Harper & Boucot 1978c), Shagamella minor (Salter) (Cocks 1978), Shaleria delicata Harper & Boucot (Harper & Boucot 1978b) and Strophoprion euglypha (Dalman) (Harper & Boucot 1978c).

SUMMARY

In this study a comprehensive quantitative analysis of the geographical and stratigraphical distribution of the faunas in the lower part of the Bringewoodian Stage (Ludlovian) in Wales and the Welsh Borderland was undertaken. Information and material was collected from 34 sections from 17 localities; over 1000 m of strata were examined and sampled using a bed-by-bed sampling technique to ensure that, as far as possible, a complete and representative picture of the faunal distribution was obtained. Over 91,000 fossil individuals were collected and identified.

For each sample, relative abundance (% of each taxon), faunal diversity and faunal density calculations were made. This data together with lithological information for all the examined sections are presented in a series of charts and tables. The accumulated data show that the shelf fauna of the lower Bringewoodian is not as homogeneous as previous less-detailed studies have suggested. The lower Bringewoodian of the 'basin' and Llandovery-Llandeilo areas was sampled for the first time in a palaeoecological investigation.

Sedimentological studies were undertaken to establish the various environments represented by the strata examined during this study. The following environments are recognised in the lower Bringewoodian of the area examined: a) proximal (in the south-east inliers) to distal (around the shelf edge) shelf environments, with a decrease in the thickness and frequency of storm deposits in the quieter water, more offshore regions b) basinal environments either with uncirculated bottom waters of low oxygen content or with bottom currents and consequently more oxygenated waters; interbedded slumps and turbidites also occur c) outer delta platform, interdistributary bay and tidally influenced distributary channel environments in the Llandovery-Llandeilo region. The hypothesis of continuous regression during the Ludlovian is rejected from the evidence of published sedimentological work and supporting observations presented herein.

The literature on the functional morphology of each individual lower Bringewoodian taxon is critically reviewed and on this, and the evidence from this study conclusions formulated regarding their autecology.

By recognising and separating transported assemblages (e.g. storm deposits, slumps or turbidite faunas) from those that show little or no signs of transportation the 'original faunal distribution' is more accurately established.

It proves possible to explain the absence, occurrence and abundance of a species by its degree of adaptation to the combined physical environmental parameters operating in each environment. These factors probably included variations in turbulence, wave buffeting, sediment reworking, sedimentation rate, substrate type, temperature fluctuations, degree of exposure and oxygenation of bottom waters with combinations of these factors operating in the various environments recognised herein. The distribution of the 9 lower Bringewoodian faunal assemblages recognised here can be similarly explained by variations in physical environmental factors.

Changes in the physical environment produced changes in fauna whereby as conditions became limiting for individual species they were excluded or became rare, whilst other species better adapted for the new environment established themselves and proliferated. Species appear to have occurred together largely where their environmental tolerances overlap. A large degree of species independence seems to have existed.

Changes in faunal density and diversity between different environments are related to the degree of stress exerted by each environment, with the highest stress conditions producing the lowest density and diversity values; the abruptness or gradation between faunal assemblages, which is controlled largely by environmental gradients, is also taken to indicate the strong influence of the physical environment on the lower Bringewoodian fauna.

CHAPTER 1

AIMS AND METHODS

AIMS

The aims of this project were to determine the geographical and stratigraphical distribution of the fauna in the lower part of the Bringewoodian Stage in Wales and the Welsh Borderlands, and to determine which factors affected faunal distribution by attempting to reconstruct the environments of the time (on sedimentological grounds) and by an examination of the functional morphology of individual taxa.

INTRODUCTION

Information was collected in a strictly quantitative way during an extensive and detailed fieldwork programme. Altogether some 91,000 faunal identifications were made during the project, these fossils being extracted from several tonnes of rock, which was broken up both in the field and the laboratory. A total of fifteen sections of lower Bringewoodian strata were examined in the field and each was subjected to intensive collecting and study. Of these five were of a 'basin facies', 3 of a 'sandy facies' in the Llandovery-Llandeilo region and seven of a 'shelf facies'. Data were obtained from a further two 'shelf' localities by examining material from the I.G.S. borehole at Brookend and the Bengry Track collections of Lawson (1973a) since this latter section has collapsed and is now completely overgrown. The geographical position of all localities from which collections were studied, and distribution of the major lower Bringewoodian facies types are shown in Fig. 1.1.

The distinction in the lower Bringewoodian (as indeed throughout most of the Ludlovian) between deposits of shelf and basin facies has long been recognised and was discussed by Holland & Lawson (1963). The shelf sediments contain an abundant shelly benthic fauna whilst the basin sediments yield a very sparse dominantly pelagic fauna and contain numerous slump and turbidite horizons indicative of accumulation in water depths greater than those covering the shelf. The basinal area was also, presumably, more unstable than the shelf since it subsided, during the lower Bringewoodian, to accumulate four to eight times as much sediment as the typical shelf thickness of about 40 m. The boundary between shelf and basin in the lower Bringewoodian is well marked by a rapid increase in thickness at the basin margin which can be seen in the isopachyte map (Fig. 1.2), although the basin succession appears to be anomalously thin

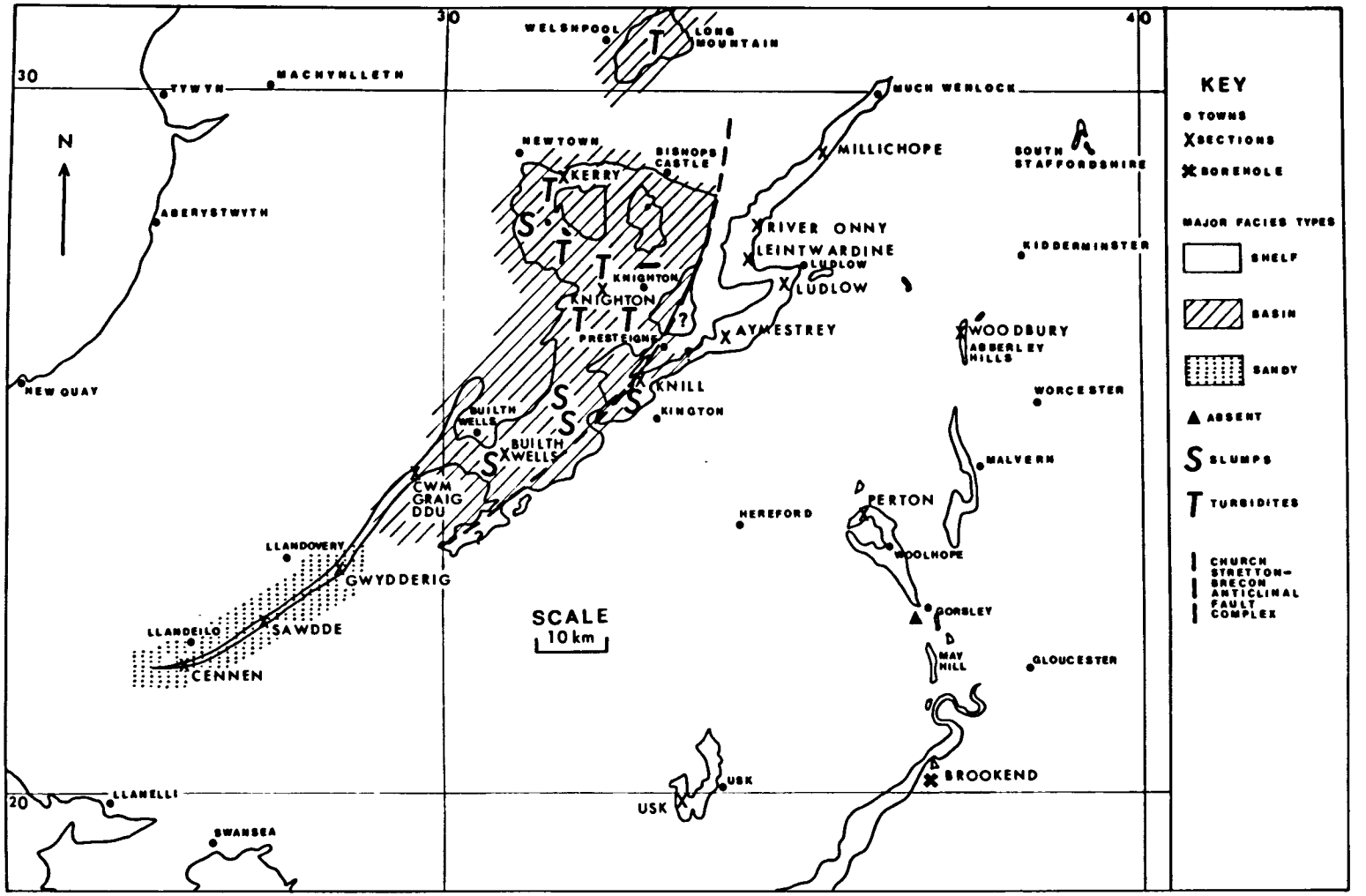


Fig. 1.1 Outcrop of Ludlovian rocks, extent of major facies types in the lower Bringewoodian and location of towns and sections examined in this study. Based on Holland & Lawson (1963) and Bailey (1969); additional information from Kirk (1948) and Palmer (1972).

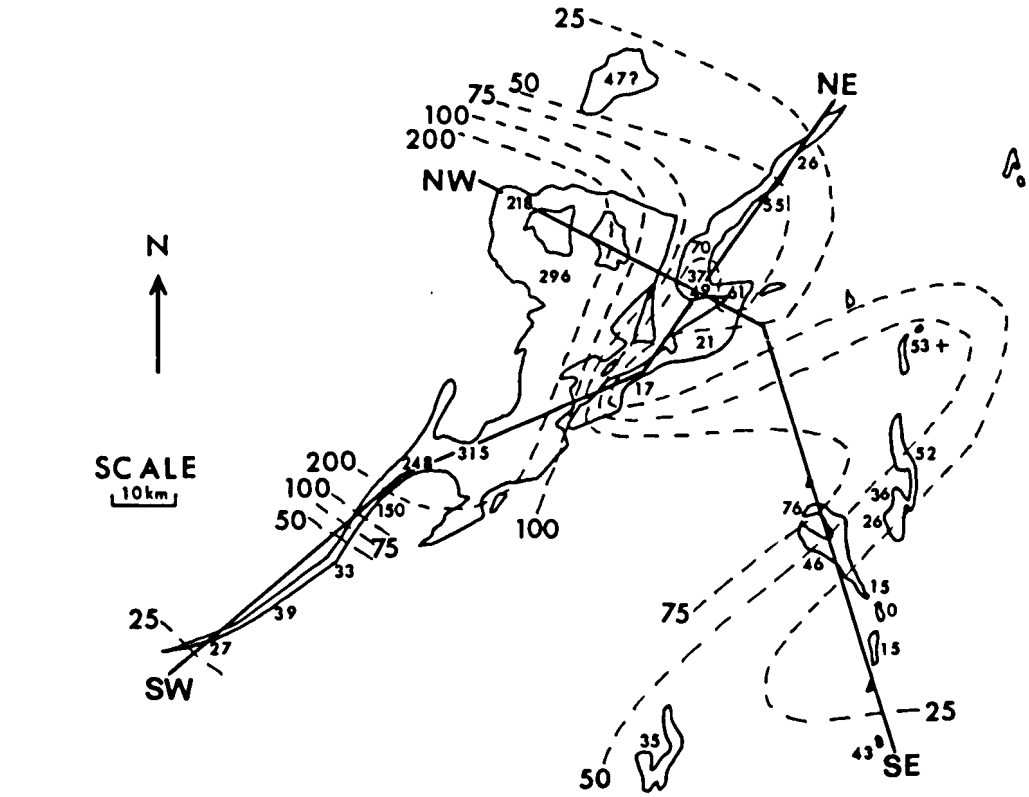


Fig. 1.2 Isopachyte map for the lower Bringewoodian. Isopach values in metres. Data from this study and also Earp (1938,1940),Holland et al.(1963),Lawson(1954,1955,1973a), R.Marsh(1976),Palmer(1972),Penn (1969),Shergold(1967), Squirrell & Tucker (1960),Straw(1937,1953),Tucker(1958) and Whitaker(1962). Lines of sections taken in Fig.1.3 are also shown.

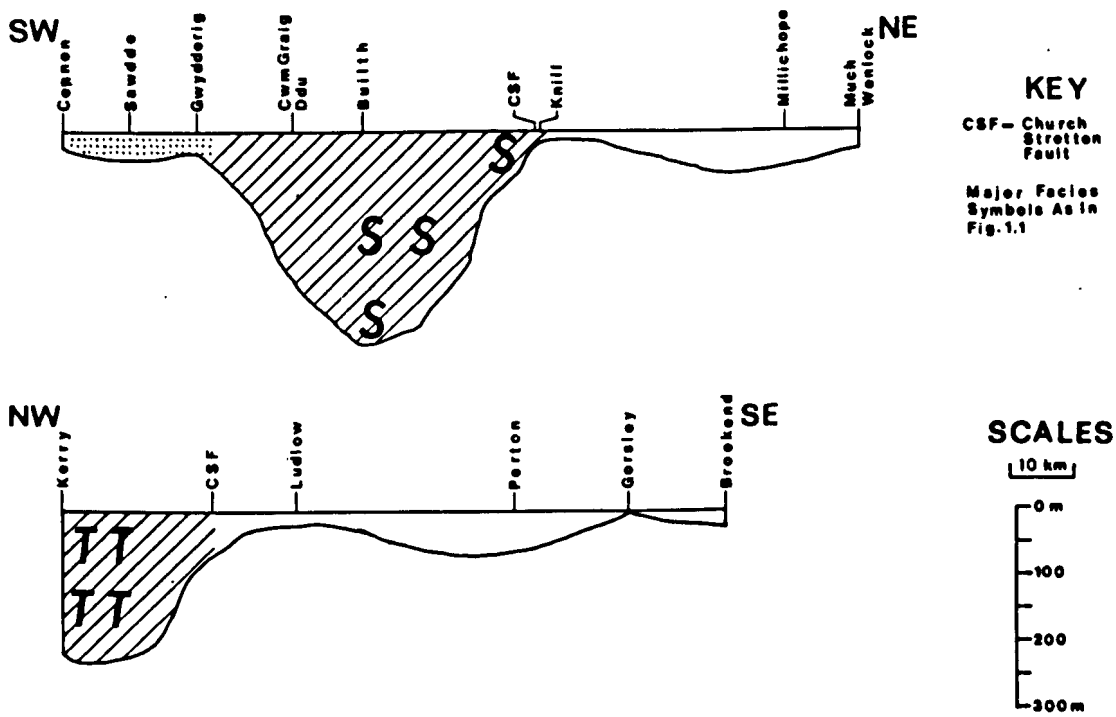


Fig. 1.3 Sections showing thickness and facies changes in the lower Bringewoodian. Lines of sections taken are shown in Fig.1.2.

in the area around Knill, a point which will be discussed later. Two sections showing thickness and facies changes across the outcrop of lower Bringewoodian strata, based on information from Figs. 1.1 and 1.2 are given in Fig. 1.3.

ESTABLISHMENT OF THE LOWER BRINGEWOOD BEDS

The Lower Bringewood Beds are a mappable division of the Ludlow Series, they are overlain by the Upper Bringewood Beds and underlain by the Upper Elton Beds. The Lower and Upper Bringewood Beds together constitute the Bringewoodian Stage at the type locality. These divisions were erected by Holland et al. (1963) during their revision of the type area at Ludlow, the divisions are mainly biostratigraphical and partly lithostratigraphical, that is they were established "mainly on the basis of their faunal assemblages but lithological characteristics have also proved very helpful in their identification" (op. cit., p.98). The base and top of the Lower Bringewood Beds are defined at standard sections in the type area, where the base of the Lower Bringewood Beds coincides with the base of the Bringewoodian Stage.

CORRELATION OF THE LOWER BRINGEWOOD BEDS

The revised type succession was correlated by Holland et al. (1963) with a) the areas of the shelf at Leintwardine (Whitaker 1962), Woolhope (Squirrell & Tucker 1960), Usk (Walmsley 1959), May Hill (Lawson 1955) and Gorsley (Lawson 1954) using graptolites as the most reliable indicators, although they are not common in the shelf facies and so the pattern of changes within the 'shelly' fauna, observed at Ludlow, was used; and b) the basinal areas of Builth (Straw 1937), Cwm Graig Ddû (Straw 1953), Knighton (Holland 1959), Bucknell (Stamp 1918), Kerry (Earp 1938) and South West Clun (Earp 1940) using mainly the abundant graptolites for correlation, since the 'shelly' faunas are very different from those of the shelf.

Cocks et al. (1971) supported the correlations of Holland et al. (1963) and also included correlations for the more recently investigated areas of Wenlock Edge (Shergold & Shirley 1968), Malvern and Abberley Hills (Phipps & Reeve 1967) and the Llandovery to Llandeilo region (Potter & Price 1965).

A correlation chart, mostly based on the work of Holland et al. (1963) and Cocks et al. (1971), is given in Fig. 1.4 for the areas where lower Bringewoodian sections were examined during this project and in which a stratigraphy had already been established.

Correlation of sections examined in this study is discussed further in the following chapters. However, it can be noted here that

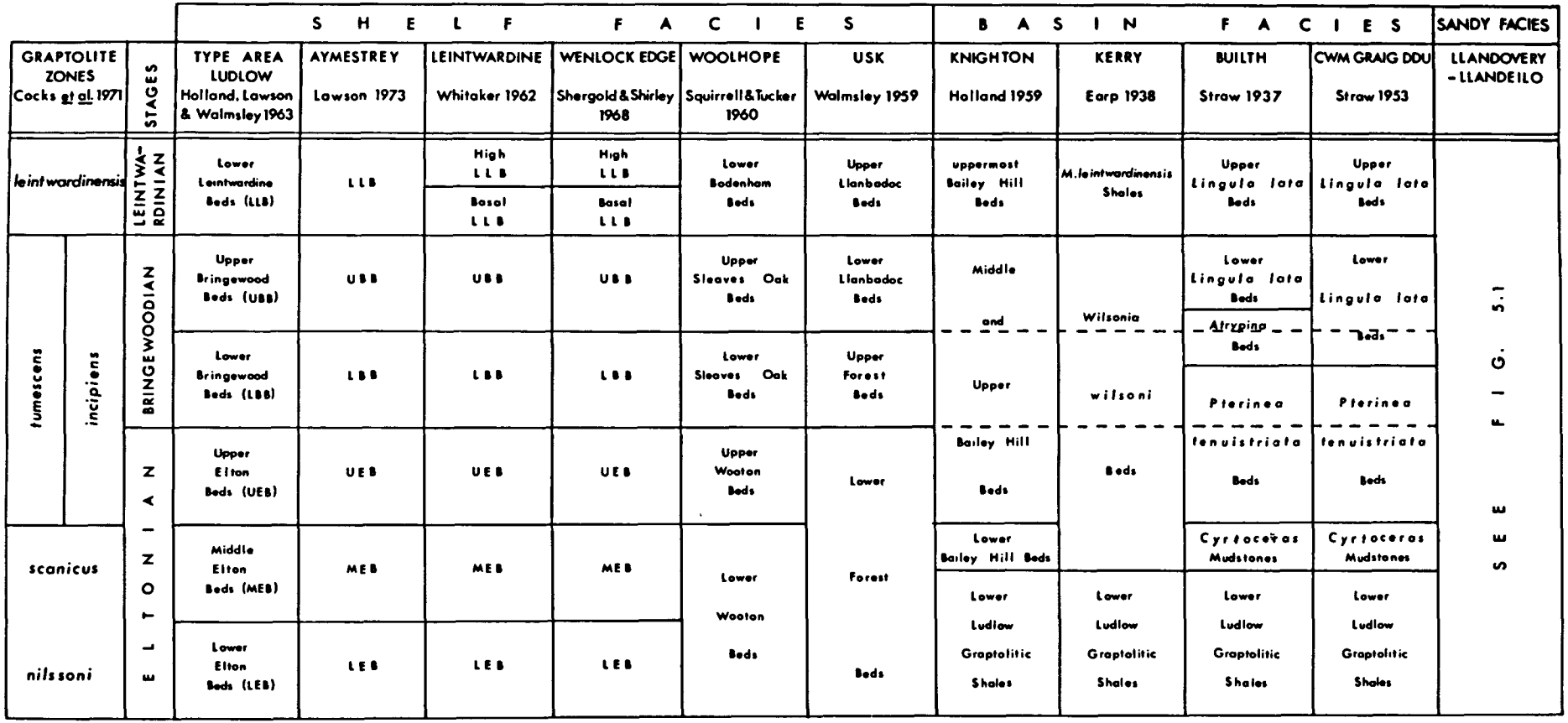


Fig. 1.4 Correlation chart for the lower Ludlovian in sections examined where a stratigraphy has already been established. Based on Holland et al. 1963 and Cocks et al. 1971.

correlation across the shelf region, mainly on the pattern of 'shelly' faunas is relatively simple. No evidence was found to support diachronism of the Lower Bringewood Beds as had been suspected by Phipps & Reeve (1967) and Walmsley (1959). In fact palynological assemblages, from many shelf localities, examined by Dr. K. Dorning (pers. comm. 1978) and graptolites recorded during this study suggest any diachronism of the Lower Bringewood Beds, if present, must be very slight.

Unfortunately correlation with and between basinal sections and localities in the sandy facies of the Llandovery-Llandeilo area is not so easy. Correlation is both difficult and uncertain in these areas as the lithology and its contained fauna is so different from the type area (and indeed the entire shelf region). Graptolites are not uncommon in the basinal sediments (and are even rarely but importantly found in the sandy facies) and it was hoped at the beginning of the project that they would be of use in establishing the basinal equivalents of the Lower Bringewood Beds. Unfortunately the graptolites were found to be poorly preserved, so that only a few were identifiable, and even the identifiable ones were often long ranging species. Therefore it was only possible, in most cases, to decide from graptolite evidence whether the beds studied were of leintwardinensis Zone age or nilssoni-scanicus Zone age, or lay between the two (i.e. were of incipiens (tumescens) Zone age). Since three divisions of the Ludlovian (Upper Elton Beds, Lower Bringewood Beds and Upper Bringewood Beds) are spanned by the incipiens Zone it was not possible to be certain from graptolite evidence that it was beds of lower Bringewoodian age that were being sampled. Palynological assemblages from basinal rocks are so depleted that they are no use for correlation (Dorning, pers. comm. 1978). Therefore due to lack of any precise means of correlation it was decided to examine the middle third of the beds lying between the Zones of nilssoni-scanicus and leintwardinensis. Obviously this is a very crude approach which assumes equal time periods for these three Ludlow divisions and constant deposition of sediment; however due to the lack of any alternative method this approach was adopted.

HISTORY OF RESEARCH

Much stratigraphical research has been carried out by numerous workers since the pioneering work of Murchison (e.g. 1839, 1854) and Elles & Slater (1906). However in a study such as this it is thought unnecessary to repeat a long list of stratigraphical workers. The interested reader is referred to the most recent work on each respective area, quoted above, which all contain comprehensive accounts of earlier studies.

Only recently have the Ludlovian rocks been examined in the field of palaeoecology. Almost all the palaeoecological work so far has been concerned with the whole of the Ludlow Series in a general overall way. Calef & Hancock (1974) examined the Ludlovian of Wales and the Welsh Borderlands using a bulk sampling technique involving the removal of large amounts of material from single beds which were widely spaced both stratigraphically and geographically. For example they looked at only three samples from three localities in the lower Bringewoodian. From their work they claimed to be able to identify five depth related brachiopod communities (cf. Ziegler 1965) which Hancock et al. (1974) suggested may span a depth range from sea level to 1500 m, although Shabica & Boucot (1976) criticised the theoretical grounds on which this estimate was based. Calef & Hancock (1974) were severely criticised by Lawson (1975) who pointed out numerous errors and mistaken assumptions in their work. Lawson (1975) described four benthic assemblages which characterise the Ludlow Stages of the shelf sequence. These included non-brachiopod benthic forms which may be locally abundant but which were ignored by Calef & Hancock (1974). Lawson (1975, p.524) claimed that his benthic assemblages give a fuller more accurate picture of the shelf faunas than Calef & Hancock's communities which he suggests give a picture which is at best an oversimplification.

Fürsich & Hurst (1975) discussed environmental factors determining Silurian brachiopod distribution and concluded that only brachiopods with more complex lophophores could live in deeper more offshore waters where they argued food was scarce.

Watkins in his work (1975, 1979) on Ludlovian benthic communities adopted a more systematic means of sampling than Calef & Hancock (1974), in which he removed samples every one metre of stratigraphic section. He examined five shelf sections through the entire Ludlovian at Ledbury, Ludlow, Woodbury, Millichope and Perton and claimed to have established six communities. Work carried out during this study has, however, revealed errors in Watkins's work, such as assigning strata to the wrong division.

Watkins & Berry (1977) suggested that the high abundance and diversity of graptolites and some associated organisms in the basin compared to their low diversity and rarity in shelf sediments was attributable to differentiation of surface water masses over these two areas. Watkins (1978a) discussed the distribution of Ludlovian bivalves with respect to their ecology.

Hurst (1978) and Hurst & Watkins (1978) claimed to be able to relate the morphology of different isorthids to their position in a series of offshore to onshore facies in the Ludlovian. However there appears to

be problems with this model which is discussed later.

Cherns (1977) examined the palaeoecology of the Lower Leintwardinian in Wales and the Welsh Borderland. Cherns (1979) has discussed the distribution and ecology of Lower Leintwardinian lingulids and presented data which suggests that it is very unlikely that Calef & Hancock's (1974) 'communities' are depth related.

COLLECTING TECHNIQUES

Obviously the collecting technique should reflect the nature of the fauna and its distribution. In almost all sections examined lower Bringewoodian faunas occurred both scattered through the rock and concentrated into bands (e.g. in coquinas or in turbidite bases). This uneven faunal distribution in the rock is not suitable for sampling set at wide intervals or a 'bulk sampling' technique (e.g. removing a large volume of material from a thickness of strata no greater than 20 cm and assuming it is typical of the whole stratigraphic division from which it was taken). Both these 'spaced' sampling procedures have been used during previous palaeoecological examinations of the Ludlovian (the former by Watkins (1975, 1979) and the latter by Calef & Hancock (1974)) and as a direct result of this not only has important data been missed but erroneous conclusions have resulted. It is believed that the only way to ensure a complete and representative picture of the Ludlovian fauna (in this case the lower Bringewoodian) is to use a bed-by-bed sampling technique, such as the one described below.

A sampling width of 0.60 m of strata was used during examination of shelf sediments. This was increased to 3.0 m for the sparsely fossiliferous sediments of the basin and sandy facies. Every bed within the sampling width was hammered and examined, the fauna recovered was recorded for the entire sample, together with any sedimentological and palaeoecological observations. If, however, any marked change took place in fauna and or lithology within a sample width then its position in the section was noted and the collections from the different lithology or faunal assemblage kept separate by giving it a separate sample number. Most lower Bringewoodian rocks contain fossils scattered throughout them, occasionally however fossils were found concentrated on bedding planes as shell sheets or in the bases of turbidites, in such cases they were treated as separate distinct samples within the main sample. In all samples an attempt to obtain at least 100 individuals was made so that quantitative analysis would not be impaired by insufficient numbers. This aim met with almost complete success in the shelf facies where it was a fairly simple matter to obtain at least this many, as the rocks were so fossiliferous. However the rocks of the basin (except in slumped beds and turbidite bases)

and those of the Llandovery-Llandeilo region (except shell beds) were so sparsely fossiliferous that it would have been impracticable to obtain 100 specimens per sample, despite increasing the sample width to 3 m. In all cases the volume of rock examined per sample was recorded so that fossil density calculations could be made later.

If a gap or the end of a section was being approached and the remaining piece of section was less than half the sample width (i.e. 30 cm for shelf or 150 cm for basin sections) then the information from that piece was incorporated into the previous sample (as long as it showed no change in lithology or fauna).

The technique was slightly modified for sections which contained recurring coquinas or slump beds. In these cases the slump or coquina was collected as one sample as was the sediment between such deposits, provided it was less than one and a half times the sample width (and contained no faunal or lithological change). This procedure saved time since (for example) if the sampling interval between two coquinas in the shelf facies was 0.70 m it would have been time consuming and uninformative to have two samples, one of 0.60 m and one of 0.10 m thickness if the fauna and lithology of both were identical.

The technique had to be further modified for the following two cases. Firstly in the Brookend borehole all fossils occurring in each 1.5 m of core were counted as one sample, except those of the coquinas which were each scored separately, because the narrowness of the core (and therefore the small volume per unit length) meant that only a few specimens were found between the many coquinas. Secondly the Bengry Track collections from Aymestrey which were examined at I.G.S. (London), where it is now stored, were collected using a 0.9 m sample width (using a technique similar to that of this study) by Dr. Lawson (pers. comm. 1977). The section has unfortunately now collapsed and is overgrown.

At the start of the project all fossil material was brought back to the laboratory for identification. Later, after a thorough knowledge of the fauna had been obtained many were identified in the field, although at least one specimen of each taxon was brought back to the laboratory to check these field identifications. The fauna of the coquinas and 'shelly turbidites' were not identified in the field since the high faunal density complicated identification. Such samples were returned to the laboratory and broken up on a rock splitter and identified under a binocular microscope; this procedure prevented both misidentification due to crowding and the concealment of smaller forms by larger ones. Lithological samples representative of each collection were always obtained. All

lithological changes and sedimentary structures noted in the field were later checked in the laboratory by examining polished sawn slabs and thin sections.

DENSITY

The volume of rock examined in each sample was recorded and the number of individuals per 5000 cm^3 calculated for each sample as a measure of fossil density. By using this arbitrary standard for all samples the comparison of fossil density both between samples of the same and different sections is possible. In examining density information it must be remembered that the mean volume of the fossils is one of the factors affecting the number in a given volume of rock. The density will also be affected by the rate of sedimentation. Despite these problems fossil density is considered a worthwhile indicator of fossil abundance.

Density measurements are unfortunately not available for the Bengry Track collections as Dr. Lawson did not record the volume of rock from which the fossils of each sample were extracted.

DIVERSITY

Two indices of diversity are used. Firstly the number of species found in each sample. Obviously this is sample size dependent and comparison between samples of different sizes is difficult. Therefore a second index was used; this is the number of species which would be obtained from a collection of 100 individuals. This can be calculated for collections with over 100 individuals by using the rarefaction technique of Sanders (1968). Where less than 100 individuals are scored in a collection the rarefaction technique is of little use (an attempt was therefore made to collect at least 100 individuals in each sample, although in sparsely fossiliferous sections this was not always possible).

PRESENTATION OF DATA

For all taxonomic categories (except crinoids, where an arbitrary figure of 300 ossicles was considered to represent one individual) the method whereby it is assumed one specimen represents one individual was adopted. For bryozoa and colonial corals each whole colony or piece of colony was considered to represent one individual. It is considered that this method does not obscure or bias the raw data, the vagaries of preservation probably cause enough bias to negate those refinements which artificial classifications (e.g. Watkins 1975, 1979) seek to develop. Trace fossils were not scored during counting although they were noted, they were obviously an important feature of the fauna when it was alive, especially on the shelf as here the sediments are completely bioturbated.

Exactly how many individuals and species of the soft bodied fauna were responsible for such bioturbation and how much was produced by benthic animals such as bivalves and trilobites is, of course, unknown.

The relative abundance of each taxon (usually species) for each sample was calculated by dividing the number of individuals of that taxon in any one sample by the total number of individuals in the same sample and expressing the result as a percentage, thus allowing direct comparison of the faunal proportions in samples of different sizes both within one section and between sections.

The relative abundance for each taxon, together with density and diversity information is plotted against a stratigraphic section indicating any variations in lithology, this is done for each sample up the section concerned.

For the sections at Ludlow, the Brookend borehole, Sawdde and Cennen and all basinal sections many samples were below 100 individuals in size and therefore rarefied diversities (i.e. the number of species which would be found in a collection of 100 individuals) are not presented on these charts, Figs. 3.5, 3.10; 4.2 to 4.5 and 5.4 to 5.5. However, the data for samples from these sections where rarefaction to 100 individuals was possible is given in Appendix I.

An asterisk against the diversity graphs for the basinal sections (Figs. 4.2 to 4.6) indicates that more than one species of graptolite was recorded from this sample, and therefore raised the diversity value, this is not obvious from an examination of the graphs as graptolites are plotted as one taxon because, due to poor preservation, they are so often unidentifiable below this level. This probably means that the recorded diversity of samples in which they are common is an underestimate of the original diversity.

APPENDICES

Appendix I contains all the raw data from which percentage abundances were calculated, together with density and diversity data. Appendix II is a faunal list of all the taxa identified during this work, together with the authors of species, referred to in the text.

CHAPTER 2

A REVIEW OF THE AUTECOLOGY OF LOWER BRINGEWOODIAN TAXA

INTRODUCTION

To explain the distribution of the lower Bringewoodian fauna it is necessary to have a knowledge of the autecology of each form. The latter can be deduced from an examination of the functional morphology both of the taxa concerned and also of related and extant forms, if these exist. This chapter therefore consists of a critical review of previous work in this field relevant to lower Bringewoodian fossils, with a summary of the main views and the present author's conclusions.

From a knowledge of both the probable life habitats of lower Bringewoodian taxa (deduced in this chapter) and the environment (as deduced from sedimentological evidence in later chapters) an attempt is made to explain the distribution of the lower Bringewoodian fauna (see following chapters).

The taxa are considered in major groups (i.e. brachiopods, bivalves, etc.) with the commonest forms discussed first.

BRACHIOPODS (ARTICULATES)

Shagamella ludloviensis

S. ludloviensis is a small chonetid. After atrophy of their pedicles adult chonetids probably rested on the convex pedicle valve for maximum stability and feeding efficiency, since in this position the anterior commissure would have been above the sediment surface, reducing the danger of sediment 'clogging' the shell (Muir-Wood 1965; Rudwick 1965, 1970; Boger 1968).

Rudwick (1965, 1970) has suggested that chonetids could, if overturned, somersault themselves back into their original position by snapping their valves together. He considered that by a similar snapping movement strophomenids such as chonetids could lift off the substrate and move posteriorly; such movements could have been used to free the shell of sediment or move away from an approaching predator. This is not to suggest that they were nektic, but rather that they could 'swim' only short distances near the bottom (Rudwick 1965, 1970; Bowen et al., 1974).

The hinge spines of chonetids may have acted as balancers or for the attachment to, or entanglement with, a foreign object (Muir-Wood 1962, 1965; Boger 1968). However, Rudwick (1965, 1970) argued these spines were sensory in function, allowing sensitive mantle material to be

extended out into the otherwise unprotected posterior direction, since they may have 'swum' in this direction it would be advantageous to 'sense' the environment ahead.

Bergström (1968) has argued that S. ludloviensis may have attached itself to benthic algae, he considered it unlikely that the species was epiplanktic because of the relatively large shell thickness, for such a small brachiopod, and the high density of the assemblages he examined which would have required an extremely large and buoyant weed to support them. However, Watkins & Berry (1977) and Watkins (1979) did suggest that S. ludloviensis led an epiplanktic mode of life when it was found in graptolitic sediments such as the Upper Elton Beds (where it is generally < 4 mm long); although they considered it led a benthic existence when it was found in bioturbated sediments with other benthic forms such as in the Lower Leintwardine Beds (where it is generally 3 to 8 mm long). Watkins & Berry (1977) suggested a modern analogue to be two species of the isopod Ianira of which the larger one is benthic and the smaller lives in Sargassum masses. However, specimens of S. ludloviensis from the Upper Elton Beds to the Lower Leintwardine Beds appear to be identical and not two different species as Watkins & Berry imply.

Raff & Raff (1970) have noted that small animals are best adapted to conditions of low oxygenation, which are interpreted later to have been present in the Upper Elton Beds. Furthermore, low oxygenation implies lack of currents which would supply nutrients and since smaller animals require less food per individual a population of them would stand a better chance of survival in such conditions. Therefore, small sized S. ludloviensis may possibly be an adaptation to conditions of low oxygenation.

In conclusion the lack of a pedicle (in adults) and the small, light shell suggest this species lived in quiet water conditions, since in more turbulent waters the shell would have been swept away. The proportionately rather massive shell commented on by Bergström (1968) might have been an adaptation to increase the weight of the shell and help stabilise it. S. ludloviensis may have been able to 'swim' short distances or may have been attached to algae on the sea floor but it seems extremely unlikely that it was epiplanktic. It appears to have been adapted to conditions of poor oxygenation and therefore low food supply.

Atrypa reticularis

Fenton & Fenton (1932a), Bowen (1966) and Copper (1967) all assumed that Atrypa lived on its flatter pedicle valve, with the convex

brachial valve uppermost (i.e. in the most hydrodynamically stable position). Due to incurving of the umbo during ontogeny the pedicle, which supported the juvenile shells, was probably atrophied (Bowen et al., 1974; Worsley & Broadhurst 1975). However Bowen et al. (1974) pointed out that if the animal lived on its pedicle valve then the commissure along the frilly border or trail (seen in many species of this genus and formed from an antereo-ventral growth of both valves) would be at or below the sediment surface, an impractical position for a suspension feeder. Therefore, they argued, as did Thayer (1974), that Atrypa probably rested on its brachial valve with the trail directed away from the sediment surface. The frilly trail probably functioned like a snowshoe preventing the shell sinking into soft sediment and also stabilising it (Fenton & Fenton 1932b; Rudwick 1965; Bowen 1966; Copper 1967; Bowen et al. 1974). The anterior fold may have functioned to separate inhalant and exhalant currents so preventing recirculation of previously filtered water (Copper 1967; Rudwick 1965, 1970). Worsley & Broadhurst (1975) considered that A. reticularis was raised by inflation of the valves during growth from a horizontal, pedically attached position (i.e. with the plane of the commissure parallel to bedding) as a juvenile to a vertical position in adulthood. The adult shells maintained such a position by partial burial of the thicker shelled, and therefore heavier, umbonal region in the sediment.

Copper (1966) considered that one of the strongest controls on the distribution of Devonian atrypids was bottom conditions. Bowen (1966) showed that interspecific variation existed in A. reticularis with shells from coarse grained skeletal limestones having abnormal brachial valves with massive shell deposits in the notothyrial cavity. He interpreted this secondary thickening as an adaptation to the moderately turbulent conditions in which these rocks were considered to have been deposited, since the thickened shell would buttress the socket walls strengthening articulation and improving stabilisation through increased posterior weight. A. reticularis from fine grained micritic argillaceous limestones have no such deposits in the notothrial cavity but have frilly trails developed (the latter being absent from the shells with notothyrial deposits) and he concluded that these were an adaptation for life in the quiet water conditions which he inferred from the lithology; the frills were thought to have stabilised the shells on a soft muddy sediment. The above two cases were considered as extremes between which all gradations existed.

Worsley & Broadhurst (1975) noted that A. reticularis populations

in the Silurian of southern Norway were of greater mean and largest shell size in shaly biomicrites rather than in silty marls. Since the largest specimens in both lithologies showed crowding of the final growth lines they were presumed to be adults and therefore the smaller shelled assemblages were considered to be stunted. They suggested that the stunted shells, which came from less calcareous and muddier rocks, were probably adversely affected by lack of turbulence and food. The larger shelled communities, which came from more calcareous and less muddy rocks, were considered to have achieved maturity at a greater shell size due to favourable conditions such as shallow well aerated waters in which atrypids thrived. However, with increased turbulence beyond that favourable for atrypids tabulate corals take over and atrypids are absent; the same occurs in the Upper Bringewoodian of the shelf edge (Newall 1966). In deeper, quieter, water turbulence is below that required by atrypids and they are replaced by other species which are better adapted to this environment.

In conclusion A. reticularis is thought to have lived with its commissure subvertical to the substrate and its weighted umbo partially buried in the sediment. It apparently required moderately turbulent environments to thrive since with decreasing turbulence the shells became stunted and finally were replaced by other forms better adapted to quiet water conditions. In more turbulent conditions the shells developed thickening of the brachial valve in the umbonal region, while in muddier environments the shells developed a flange to support themselves on the soft substrate. The strongly biconvex ribbed shells show good adaptations to moderately turbulent environments.

Mesopholidostrophia cf. lepisma

M. cf. lepisma is a smooth shelled pholidostrophid which was pedically attached only as a juvenile. Later in life the pedicle atrophied and the adults presumably lay unattached on the sea floor (Williams 1953; Hurst 1974). They were not pedically attached as adults, since they had no pedicle opening, as claimed by Ziegler et al. (1968). The shells probably rested on the convex pedicle valve, for maximum stability and feeding efficiency; with the umbonal secondary shell deposits producing a centre of gravity which was postereo-medianly situated. These features would have served to raise the anterior commissure above the sediment surface so that sediment was kept out of the lophophore tract. The mucronate hinge line allowed the presentation of a larger area to the substrate so inhibiting overturning of the shell in the case of disturbance by currents (Williams 1953; Rudwick 1965, 1970; Hurst 1974). Further-

more, the extension of the hinge line would have prevented the lateral part of the commissure from becoming inundated with sediment as the wing would have acted as a pivot and constantly elevated the lateral commissure above the substrate (Hurst 1974). If the shell had been overturned it could probably have righted itself quickly by snapping its valves together (Williams 1953; Rudwick 1965, 1970). A similar snapping of the valves may have resulted in the shell 'swimming' short distances if it was buried in sediment or threatened by predators (Rudwick 1965, 1970; Bowen et al. 1974) although, its quite strong concavo convex shape suggests the latter may have been unlikely.

Therefore the fairly small size, lack of adult attachment and absence of ribbing and extensively developed secondary shell deposits suggests that the species lived in only moderately turbulent environments, since it shows no adaptation to either very turbulent or very quiet conditions.

Leptostrophia filosa

Leptostrophids are biplanate stropheodontids which lost their pedicle during ontogeny and so must have lain free on the sea floor as adults. The large area to shell volume ratio and mucronate hinge line are probably adaptations to present the largest area of shell to the sediment surface. As no part of the shell would have projected up into the water for currents to act on leptostrophids were probably able to lie on the sediment in a fairly constant state of rest (Williams 1953). The close proximity of the commissure to the sediment surface suggests that they may have been tolerant of sedimentation. Williams (1953) commented that the power of the muscles must have been magnified by the large area of shell in relation to volume, therefore by 'clapping' their valves together they could probably have 'swum' so clearing themselves of sediment very easily (Rudwick 1965, 1970; Bowen et al. 1974).

A further adaption to living close to the sediment surface is shown by the development of closely spaced fine costae which Rudwick (1965, 1970) considered corresponded to the position of mantle setae. The fine ribbing pattern of L. filosa suggests that these setae were closely spaced and must have formed a closely spaced sensitive grill, which could warn of the approach of any harmful sediment which would damage the delicate feeding and respiratory organs so that the animal could snap shut its shell before any harm was done.

Ziegler et al. (1968) found Leptostrophia to be most common in the nearshore Eocoelia 'community'. They were found, normal to bedding, disarticulated and in variable orientations in a lens shaped body. Despite

the fact that they noted that Seilacher & Meischner (1964) had interpreted such deposits from the Oslo area as transported coquinas, Ziegler et al. (1968) considered that these deposits represented undisturbed assemblages and Leptostrophia was interpreted as living upright, pedically attached at 90° to bedding, on death the valves were thought to have reorientated while remaining normal to bedding. However, if the shells had lived so close together they would have shown signs of growth deformations as Williams (1953) suggested and Ziegler et al. (1966) noted in a closely packed life association of Pentamerus. Besides, Leptostrophia could not have lived vertically as Ziegler et al. (1968) claimed, since as an adult it had no pedicle opening (Muir-Wood & Williams 1965; Williams 1953; Rudwick 1965, 1970) and would therefore have been completely unstable in this position.

In conclusion therefore Leptostrophia showed good adaptations for living close to the sediment surface, where its very flat shape would have made it difficult to move; it may therefore have been able to live in moderately turbulent water. However, it showed no obvious adaptations for very turbulent or quiet waters.

Leptaena depressa, Strophonella euglypha and Amphistrophia funiculata

All these species show a marked geniculation of the valves, because of their similar shell form they are thought to have had similar life styles. Rudwick (1965, 1970) argued that shells with this form were probably adapted for a sessile semi-infaunal mode of life with the shell sunk into the sediment, giving stability to the shell as well as camouflaging it from predators, with only the valve margins held free of the substrate for feeding and respiration. Shiells (1968) during a discussion on the functional morphology of the productid Kochiproductus noted the tendency of such geniculate shells to accumulate silt in the visceral cavity during the intake of water for food and respiratory purposes. However, the fine ribbing on all these shells is again considered to have accommodated sensory setae at the commissure (Rudwick 1965, 1970) which would detect such silt and trigger the closure of the shell before it was 'inhaled'.

S. euglypha has a large thick heavy shell with internal thickening, these adaptations are probably to prevent overturning of the shell by currents (Rudwick 1965, 1970). It therefore shows good adaptations to turbulent environments.

L. depressa also has a large, thick heavy shell with internal thickening probably to prevent overturning by currents (Rudwick 1965, 1970). The strong concentric rugae serve to strengthen the shell and

indicate that this species may have lived in quite turbulent conditions. Muir-Wood & Williams (1965) note that Leptaena possessed a pedicle throughout ontogeny. However, adult shells of L. depressa have only a very fine pedicle opening and although Thayer (1975b) has shown that the strength of the pedicle is not proportional to the diameter of the foramen it is unlikely that a pedicle as thin as that of L. depressa would have functioned as anything other than a weak tether for the shell (Rudwick 1965, 1970).

A. funiculata lacks the large, massive and reinforced shells of the above species and was probably unable to live in such turbulent conditions. However, the finer ribbing developed on the shell probably indicates the existence of a more sensitive grill of setae at the commissure capable of detecting finer particles than those of the former two species.

In conclusion therefore, A. funiculata probably lived in quieter, possibly siltier environments than S. euglypha or L. depressa, which were well adapted to quite turbulent waters.

Sphaerirhynchia wilsoni and Microsphaeridiorhynchus nucula

Ager (1962, 1965) and Thayer (1974) suggested that rhynchonellids which were found in argillaceous sediments with a pelagic fauna (and an absence of any true benthic forms) had been rafted in on a Sargassum type alga to which they had been attached. Bowen et al. (1974) noted that in New Zealand the modern rhynchonellid Notosaria occurs as clusters with the beaks crowded about the point of attachment which is often the holdfast of a marine alga which may be uprooted and transported onto beaches or into deeper water with the Notosaria still attached. Cocks & McKerrow (1978) have suggested that sea weeds probably provided the best anchorage for M. nucula. The widespread distribution of Leiorhynchus and Camarotoechia in the Upper Devonian of New York was explained by storms ripping up algae on which gregarious clusters of these shells lived and transporting them over a large area (Bowen et al. 1974).

S. wilsoni is a globose strongly ribbed rhynchonellid whose robust shell seems to have been well adapted for turbulent conditions (Stel & Coo 1977). The species has a foramen and Westbroek et al. (1975) considered that it was pedically attached, resting with its brachial valve on the sediment. The fold and sulcus was probably a device for separating inhalant and exhalant currents (Rudwick 1964, 1965, 1970; Westbroek et al. 1975). The zig zag commissure and development of marginal spines, to form a grill, have been interpreted as protective devices to exclude silt from the mantle cavity (Rudwick 1964). Westbroek et al. (1975) considered that the development of marginal spines corresponded to geniculation of the brephic shell to produce the globose form.

M. nucula is a globose rhynchonellid with thick rounded ribs and a large apical foramen. Stel & Coo (1977) concluded from the strongly ribbed robust shell, its encrustation with algae and its occurrence with oolites in the Silurian of Gotland that M. nucula lived in shallow turbulent conditions. Ziegler et al. (1968) and Cocks & McKerrow (1978) noted that this species was the only abundant articulate brachiopod in their most near shore Lingula 'community', and suggested, as had Thayer (1974), that it may have been more euryhaline than any other brachiopod. Ager (1965) also indicated that (Mesozoic) rhynchonellids may have had some degree of tolerance to lower salinities since they persisted further than any other groups in the transition from fully marine to fully non marine deposits. Ager (1965) also considered that thick shells with strong ribbing and a large pedicle opening were ideally adapted for shallow rough environments. It is therefore notable that M. nucula is found in the Welsh Borders up to the basal Downtonian and therefore preferred or could tolerate such shallow water proximal environments. The sulcus and fold and the zig zag commissure are interpreted as devices for separating inhalant and exhalant currents and excluding particles from the shell respectively; see above discussion of the functional morphology of S. wilsoni.

In conclusion, both S. wilsoni and M. nucula are well adapted to high energy environments in which they may have lived attached to algal fronds. M. nucula may have been able to tolerate lower salinities than most brachiopods.

Gypidula lata and Gypidula galeata

Gypidulids are biconvex pentamerids with a well developed pedicle fold and brachial sulcus. G. lata is small and smooth while G. galeata is large and ribbed. Anderson & Makurath (1973) examined gypidulan assemblages from the Silurian and Devonian of the U.S.A. They found assemblages which they thought to be in life position, the Gypidula's were orientated beak down and as they lacked a pedicle opening (as the Ludlovian ones did) they were assumed to be free living with the massive secondary shell thickening of the umbonal region, especially the posterior of the pedicle valve, serving to anchor the shells and raise their anterior commissure high above the substrate (Rudwick 1965, 1970). The fold and sulcus was probably a development to separate inhalant and exhalant currents, so preventing recirculation of previously filtered water (Rudwick 1965, 1970).

Anderson & Makurath (1973) and Makurath (1977) considered that the above adaptations were ideal for occupying biogenically reworked,

occasionally shifting substrates, near wave base in an open shelf environment. They found that the greatest abundance of gypidulids was in sediments thought to have been deposited in such an environment. They were absent from high energy barrier conditions and also from low energy offshore environments well below wave base where conditions were thought to have been too quiet.

In conclusion, Gypidula appears to be well adapted to moderately turbulent environments but not to quiet water or high energy conditions.

Isorthis orbicularis and Salopina lunata

Both these species are enteletaceans with a shallow sulcus in the brachial valve which may have functioned to separate inhalant and exhalant currents and prevent recirculation of previously filtered water (Rudwick 1965, 1970). Both have a foramen throughout life and therefore presumably possessed functional pedicles for anchorage, and may have required a hard site for attachment, although Rudwick (1961) considered that some brachiopods might have had a root-like pedicle for anchoring into soft substrates. The shells of both species are finely ribbed and Rudwick (1965, 1970) has suggested that such ribs correspond to the position of mantle setae which formed a sensitive grill, capable of triggering the closure of the shell upon the approach of 'harmful particles', thereby protecting the animal.

I. orbicularis. Hurst & Watkins (1978) used statistical methods to analyse populations of dalmanellid brachiopods. They concluded that many of the Ludlovian Isorthis species and subspecies described by Walmsley (1965) and Walmsley & Boucot (1975) showed continuous variation in many characters and were therefore part of the same species group, which they termed the I. clivosa species group (this included I. orbicularis as one end member of the variation).

Hurst & Watkins (1978) and Hurst (1978) claimed they could recognise a correlation between dalmanellid morphotypes and inferred environments through a series of offshore to onshore facies. They proposed that offshore and nearshore dalmanellid populations had definite distinctive features between which all gradations existed. For Isorthis they claimed a continuous change due to prograding from I. clivosa in offshore Eltonian strata to I. orbicularis in nearshore Lower Leintwardine Beds. They considered I. clivosa was the commonest isorthid of the Lower Bringewood Beds. However, Walmsley (1965, p.473) in his original description of these species noted that it was I. orbicularis that was abundant in these beds with I. clivosa being extremely rare. All the isorthids collected from the Lower Bringewoodian shelly facies during this study are far more

like I. orbicularis than I. clivosa. Both Hurst (1978, Plate 58, Figs. 16 to 19) and Hurst & Watkins (1978, Plate 1, Figs. 17 to 24) figure I. clivosa from the Lower Bringewood Beds. However the grid reference given for their location (in both cases SO 71313858) indicates that they have been collected from the wrong strata, since the west side of Knapp Lane Quarry, where they come from, exposes Lower Leintwardine Beds and not Lower Bringewood Beds (Phipps & Reeve 1969; Penn 1969; Penn et al. 1971) a fact confirmed by the author's personal examination. Although Watkins (1979) claims to have found 'typical' Lower Bringewoodian fossils from these strata none have been recorded by any of the authors quoted directly above. Therefore Watkins's claim is treated with some degree of scepticism and the strata on the westernmost side of Knapp Lane Quarry are considered to be Lower Leintwardinian. If this is so then the most 'nearshore' and some of the most 'offshore' dalmanellids come from the same beds (the Lower Leintwardine Beds) which seems to throw serious doubt on the validity of the model. Further, Hurst (1978) and Hurst & Watkins (1978) assumed that the Lower Leintwardine Beds were deposited in shallower water than any of the underlying Ludlovian divisions, as suggested by Calef & Hancock (1974). However, Lawson (1975) has shown that all the evidence (both faunal and sedimentary) supports Phipps & Reeve's (1967) hypothesis that the Upper Bringewood Beds were deposited in shallower water than the Lower Leintwardine Beds. Therefore if Hurst (1978) and Hurst & Watkins (1978) were correct the nearest shore dalmanellids should be found in the Upper Bringewoodian with more offshore forms in the Lower Leintwardinian, instead the reverse is the case and therefore the model seems untenable.

S. lunata. The persistence of this form up to the Downtonian in the Welsh Borders suggests a preference for shallow water environments; it may even have been slightly euryhaline since it commonly occurs with M. nucula.

In conclusion the absence of I. orbicularis from the upper Ludlovian in which S. lunata thrived may indicate a preference for relatively less turbulent environments. However, both S. lunata and I. orbicularis are very similar morphologically and it is conceivable that the absence of I. orbicularis in the upper Ludlovian can be explained by its possibly less euryhaline nature. Both species are ribbed and pedically attached and appear to be well adapted to quite turbulent environments.

Protochonetes ludloviensis and P. minimus

After atrophy of their pedicles these chonetids probably rested on their convex pedicle valve, so that their concave convex shape kept the

anterior commissure above the sediment, reducing the danger of sediment 'clogging' the shell (Muir-Wood 1965; Rudwick 1965, 1970; Böger 1968). If overturned these shells could probably have regained their original position by snapping their valves together (Rudwick 1965,1970). By a similar snapping of their valves these shells may have been able to 'swim' short distances to avoid predators or free themselves of sediment (Rudwick 1965, 1970; Bowen et al. 1974).

The hinge spines may have acted as balances or for the entanglement or attachment of the shell to a foreign object (Muir-Wood 1962, 1965; Böger 1968) or they may have had a sensory function, projecting sensitive mantle material into the otherwise unprotected posterior direction, into which they would move on clapping their valves (Rudwick 1965, 1970).

The shells of both species are finely ribbed, Rudwick (1965, 1970) has suggested that such ribs correspond to the position of mantle setae at the commissure which formed a sensitive grill capable of triggering the closure of the shell upon the approach of 'harmful particles', thereby protecting the organism.

P. ludloviensis appears to have a high tolerance or preference for shallow, nearshore environments since it is found up to the base of the Downtonian which probably marks the change from marine to non-marine deposition. Cocks & McKerrow (1978) have proposed that it may have been euryhaline.

P. minimus has a small light shell and since it lacked a pedicle as an adult would have been easily swept away in turbulent water, it therefore probably preferred quiet water conditions. Its small size probably means it was adapted to conditions of below normal oxygenation and food supply in quiet water environments (see discussion of S. ludloviensis).

Dayia navicula

D. navicula is a small smooth unequally biconvex spiriferid. The incurvature of the umbo during ontogeny leads to the loss of a functional pedicle in the adult. Alexander (1947) and Tucker (1964) considered that D. navicula rested on its heavier pedicle valve which shows extensive thickening of the secondary shell layer, especially in the umbonal region. This thickening would have stabilised the shell and raised the anterior commissure above the sediment (Rudwick 1965, 1970). The fold (ventral) and sulcus (dorsal) are probably developed to separate incoming and exhalant currents, so preventing recirculation of filtered water (Rudwick 1965, 1970).

Tucker (1964) looked at thin limestone bands containing abundant

D. navicula in Downton Gorge, Shropshire. He concluded that D. navicula lived in quiet conditions in which little silt was in suspension as he considered that the limestones in which they were found were primary. Cherns (1977), however, examined these beds and found them to be coquinas in which the calcareous matrix was secondarily derived from the abundance of closely packed shells. From a detailed study of D. navicula in the Lower Leintwardinian she concluded that it lived in quiet water distal shelf environments, where it could probably tolerate sedimentation. The lack of pedicle (in the adult) and the small shell suggest it would have been swept away in turbulent conditions. Its small size means it was probably well adapted to conditions of below normal oxygenation and food supply in very quiet water environments (see discussion of S. ludloviensis).

Hyattidina canalis

This is a small smooth spiriferid which in many ways resembles D. navicula. However, it has a ventral sulcus and dorsal fold. Cherns (1977) considered that H. canalis was pedically attached throughout life but Alexander (1947) noted that the umbo incurved during ontogeny so that it concealed the foramen in the adults which became unattached. The adult shells show extensive thickening of the shell in the umbonal region which would have stabilised them and kept them in position. H. canalis is thought to have lived in the same sort of environment in which D. navicula flourished since it shows similar adaptations.

Howellella elegans

H. elegans is a small biconvex spiriferid with a fold and sulcus, which Rudwick (1965, 1970) interpreted as a device for separating inhalant and exhalant currents, so preventing the recycling of previously filtered water. The open foramen suggests H. elegans was pedically attached throughout life, possibly to a solid object, although Rudwick (1961) has shown that some brachiopods have root-like pedicles which can anchor into soft substrates. The very strong ribbing suggests an adaptation to agitated environments since it would have strengthened the shell. Its persistence into the highest Ludlow beds in the Welsh Borderland, which are overlain by the non-marine Downtonian sediments, suggests a preference for nearshore, proximal environments. Ager (1965) considered that thick shells which were strongly ribbed with large pedicle openings were ideally adapted for shallow, rough water conditions. The zig zag commissure was interpreted by Rudwick (1964) as a device to prevent silt getting into the shell.

H. elegans therefore appears to be well adapted to turbulent conditions.

Kirkidium knightii

K. knightii is a very large biconvex pentamarid whose umbo became so incurved that in adults no passage for a pedicle remained. However, the immense secondary thickening of the shells, especially in the posterior of the pedicle valve, would have served to anchor the shell and orientate the anterior commissure away from the substrate (Newall 1966; Rudwick 1965, 1970). The coarse ribbing served to strengthen the shell and it was probably able to withstand very turbulent conditions. These shells occur as 'banks' in the Upper Bringewoodian of the shelf edge areas which Newall (1966) interpreted from palaeoecological and sedimentological investigations to represent the most turbulent conditions during the deposition of this division, possibly even forming in the breaker zone. Newall (1966) also noted that in siltier lithologies, probably deposited in less turbulent conditions, that the shells of this species were significantly smaller (stunted or consistently younger at death); this suggests a requirement for clear water and greater turbulence.

Aegiria grayi

A. grayi is a small concavo convex plectambonitacean with a foramen large enough to have contained a functional pedicle (Cocks 1970). An epiplanktic mode of life has been suggested for its close relatives Sericoidea and Chonetoidea (Bergström 1968). The very thin light shells were considered to be ideally adapted to such a mode of life. Sheehan (1977) has, however, argued that the thin shells are due to low nutrient levels, since they are found in what are interpreted as deep water environments and that the density of the shells in these supposed epiplanktonic assemblages would have weighed down the algae so much that they would have sunk. Sheehan therefore argued that the shells had attached themselves to alga after it had fallen to the sea floor. A. grayi is abundant in the Llandovery Clorinda 'community' and Cocks (1970) has suggested it lived attached to algae at the depth inhabited by this community; he further suggested that these algae may have been uprooted occasionally and transported (with A. grayi still attached) into environments inimical to brachiopods. Cherns (1977) considered that the small light valves of A. grayi were well adapted for an epiplanktic existence. She argued that its Lower Leintwardinian distribution, centred on the basin (in which benthic forms were absent) and outermost shelf also suggested an epiplanktic life style. Its absence from the inner shelf was explained by either selective destruction of the small light valves in the more agitated environment or as an original distribution feature. However, she did not rule out the

possibility that it may have lived attached to benthic algae in the shelf edge region which, during storms, may have been periodically ripped up and transported out into the basin with A. grayi still attached.

It therefore appears that A. grayi may have been attached to either floating weed or algae living on or sunken to the sea floor.

Eospirifer radiatus

E. radiatus is a large biconvex spiriferid with a strong fold and sulcus, probably for separating inhalant and exhalant currents, so preventing the recirculation of previously filtered water (Rudwick 1965, 1970). The open apical foramen throughout ontogeny indicates a permanent pedically attached mode of life, possibly to hard objects, although they may have possessed a root-like pedicle for anchorage in soft substrates (Rudwick 1961). The ribs probably strengthened the large, heavy, thick shell and it appears to be well adapted to moderately turbulent conditions.

Shaleria sp. nov. and Coolinia pecten

Shaleria is a stropheodontid while Coolinia is an unattached davidsoniacean. However, both shells show similar features and are therefore thought to have had similar modes of life. Both are unattached as adults having lost a functional pedicle during ontogeny (Muir-Wood & Williams 1965). The flat, broad, slightly concavo convex shells are well adapted for an unattached mode of life; they probably lived on the convex pedicle valve, with the concavo convex growth form maintaining the anterior commissure above the sediment surface, preventing the shell being 'clogged' by sediment (Rudwick 1965, 1970). If the shells were overturned by bottom currents then by snapping their valves together they were probably able to quickly somersault back into their original position, by a similar snapping of the valves they were probably able to 'swim' short distances, posteriorly, to avoid being buried in sediment or to escape from predators (Rudwick 1965, 1970). Both species have finely ribbed shells and Rudwick (1965, 1970) suggested that such ribs correspond to the position of mantle setae which formed a sensitive grill , capable of triggering the closure of the shell upon the approach of 'harmful particles', and so protecting the organism.

Both species are devoid of adaptations to either low or high energy environments.

BRACHIOPODS (INARTICULATES)

Lingulids

Lingulids from the Bringewoodian have the same morphology as recent infaunal forms, and articulated valves are commonly found at 90°

to the bedding (anterior uppermost) apparently in situ; they are therefore thought to have had the same mode of life. Although Craig (1952) and Newall (1970) assumed that lingulids used their pedicles for burrowing Thayer & Steele-Petrović (1975) showed that modern forms enter the substrate with the shell anterior first and burrow with a scissor-like motion of the valves, the pedicle acting to support the shell, after lifting it into position. The burrow is 'U'-shaped with the animal ending anterior upwards with the pedicle extending back down the burrow. They suggested that all fossil lingulids burrowed in this manner. Szmuc et al. (1976) and Hakes (1976) have described lingulid trace fossils (Lingulichnus) but only the ascending part of the burrow is preserved, presumably the descending part of the 'U' burrow quickly collapses.

Modern lingulids are found in warm very shallow shelf seas at depths of usually less than 40 m (Craig 1952; Paine 1970); because of this fossil forms are usually considered to indicate shallow water deposits (e.g. Ziegler et al., 1968). However some modern species have their greatest abundance in fairly deep water, e.g. Glottidia albida which may be found in water up to 147 m in depth (Mattox 1955; Paine 1970). In the fossil record lingulids have been reported from deep water sediments (e.g. Ziegler et al., 1968; Bowen et al., 1974) but such occurrences have been considered unusual and explained in the following ways. Bulman (1964) suggested that the lingulids found in some Silurian graptolitic shales were giant larvae resulting from delayed settling due to adverse conditions. Bowen et al. (1974) found linear aggregates of lingulids in 'anaerobic' shales and considered they had been brought in attached to plant material. Watkins & Berry (1977) argued that Lingula lata found in the Ludlovian basinal sediments was probably epiplanktic. Pickerill (1973) found Ordovician lingulids at 90° to bedding in presumed life position, in what he regarded was an offshore deposit and suggested they may represent a successful spat full in an atypical site.

Craig (1952) noted that lingulids were unusually euryhaline (for brachiopods) as they occurred in nearshore brakish water, while Cloud (1948) noted their high tolerance for environments with a low oxygen content.

Cherns (1977, 1979) reviewed the ecology of lingulids and examined their distribution in the Lower Leintwardinian of Wales and the Welsh Borders. She found that Lingula lewisii was confined to the shelf areas while Lingula lata was found in basinal sediments, the distribution of the two species overlapping only in the outermost shelf edge region. Both species were found at 90° to the bedding in assumed life position and as no specimens of L. lewisii were found in basinal sediments, or L. lata

on the shelf proper, it was concluded this distribution was an original feature. The shells of L. lata and L. lewisii were examined in detail and their existence as separate species confirmed, so that L. lata cannot be considered a stunted form of L. lewisii in an unfavourable environment. The basinal sediments in which L. lata occurs have no other benthos, are well laminated with few signs of bioturbation and have a limited pelagic fauna. Cherns (1977, 1979) concluded that conditions in the basin must have been inimical to most benthos, possibly due to low oxygen levels. L. lata was evidently adapted to such environments and could tolerate the low oxygen levels (Cloud 1948) and the high turbidity and constant sedimentation (Thayer & Steele-Petrović 1975) that seem to have existed. Its occurrence in these sediments was therefore not the result of spat falls on atypical sites (cf. Pickerill 1973) or giant larvae (Bulman 1964). As L. lata was found in life position in burrows in basinal sediments (Cherns 1977) it was clearly not epiplanktic as suggested by Watkins & Berry (1977).

In conclusion L. lewisii appears to have been adapted to the shelf environment but was unable to tolerate the poorly oxygenated environment which L. lata appears to have preferred.

Orbiculoidea rugata

Rowell (1965) considered that the pedicle was functional throughout life, although only a small foramen was present in adults. Thayer (1975b) has, however, shown that the strength of the pedicle attachment is not directly related to the diameter of the foramen. Orbiculoidea may have attached to hard objects although it may have had a root-like pedicle for anchorage in soft substrates (Rudwick 1961). Cocks & McKerrow (1978) have suggested that Orbiculoidea may have lived attached to floating algae.

Craniops implicata

Craniops lacked a pedicle and attached itself to solid foreign objects by cementation of the apical region of the pedicle valve, as in the modern form Crania (Rowell 1965). C. implicata therefore may have required a hard site for attachment.

BIVALVES

Actinopteria pleuroptera, Pteronitella sp., P. retroflexa, Limoptera reticulata and Tolmaia sowerbyi

These all belong to the family Pterineidae. They are all very similar in morphology with prosocline shell forms, broadly rounded lobate anteriors, well developed posterior wings and a shallow byssal notch associated with a lobate or poorly developed anterior auricle. The right

valve is slightly less convex than the left valve, but not as markedly so as modern pteriaceans. The two valves have slightly different ornamentation patterns.

Modern pteriaceans are epibyssate and have a well developed anterior auricle which serves as a stabilising device to prevent overturning of the shell. The right valve, which is undermost, is normally flattened to lower the angle of elevation of the sagittal plane for improved stability against disruptive water movement (Stanley 1970, 1972). However the Ludlovian pterineids, described above, show moderately inflated, nearly equivalve shells, with poorly developed anterior auricles (reduced or rounded) which could not have prevented the shell from being overturned. They have shallow byssal sinuses and rounded ventral margins. These shells could not possibly have rested stably in an epifaunal position on the rounded ventral margin, nor could they have lived epifaunaly on the convex right valve without being overturned easily by water movements. In fact these shells show all the adaptions of endobyssate species as noted by Stanley (1970, 1972). The inequivalve ornamentation of Actinopteria (right valve smooth) and the slightly inequivalve nature of Pteronitella and Tolmaia (right valves flatter) suggest these taxa lived with their sagittal plane not vertical and the right valve lowermost. This low angle of fixation was probably for stability in less deeply buried life positions (Stanley 1972). Kauffman (1969) considered that the posterior wing aided the animal by acting as a rudder and swinging it parallel to the environmental water flow which would aid feeding and water removal. Stanley (1970, 1972) however rejected this idea since living shells with posterior wings are not found to orientate parallel to water flow. Instead he argued that the posterior wing acted to separate inhalant and exhalant currents so that waste from the exhalant current would not be carried by the environmental water flow into the inhalant current. Stanley (1972) was able to substantiate this conclusion with flame experiments.

Pterinea tenuistriata

The posterior auricle is less well developed, while the anterior one is better developed than in the shells discussed above. The shells are remarkably thin, almost smooth and very small. Stanley (1972) described the life habitat of Pteria colymbus. This shell has extended posterior and anterior wings and is found attached to plants (sea whips). It is gregarious with many individuals clustered around one stem. He noted that even after uprooting of the plant by a storm the byssal attachment of P. colymbus was so strong that the shells were still attached. Cherns (1977) noted that the distribution of P. tenuistriata was similar to

that of the graptolites, being most abundant in the basin where they occurred in laminated shales in which no benthos was found and which may have been deposited in anoxic conditions. She therefore argued that the species was epiplanktic, bysally attached to floating algae. R. Marsh (1976) and L. Marsh (pers. comm. 1977) also consider that P. tenuistriata was epiplanktic. The small thin shell would be ideally adapted for this life style. Similar arguments have been used to suggest an epiplanktic mode of life for posidonids (see Stanley 1972; Jeffries & Minton 1965). Cherns (1977) suggested the absence of this species from the sediments of the shelf area, was possibly due to an original distribution over the basin or that the small light valves may have been broken up in the more agitated waters of the shelf. Therefore P. tenuistriata appears to have been epiplanktic.

Cardiola cornucopiae

Berry & Boucot (1967) noted that the distribution of Cardiola was very similar to that of graptolites in Europe and N. Africa. They found the genus in both offshore deposits where it occurred almost exclusively with graptolites (and virtually nothing else) and in nearshore deposits with other species of bivalves, other benthic animals and graptolites. Such a distribution would appear to indicate an epiplanktic mode of life for Cardiola. However, McAlester (in Berry & Boucot 1967) considered Cardiola was epifaunal.

Watkins & Berry (1977) also noted the association of praecardiacean bivalves and graptolites together and considered their similar distribution over Europe and N. Africa as evidence for paraecardiaceans living bysally attached to floating algae. This life style has been suggested for the praecardiacean Butovicella by Kříž (1969). Butovicella is very similar in gross shell morphology to Cardiola.

R. Marsh (1976), Cherns (1977), Watkins (1978) and Cocks & McKerrow (1978) have all commented on the occurrence of Cardiola with graptolites in parallel laminated shales which contain no benthic forms and may even have been deposited in anoxic conditions. They all therefore suggested that Cardiola was epiplanktic. Similar arguments have been used by Stanley (1972) to suggest that posidonids were epiplanktic. It is concluded, therefore, that Cardiola was almost certainly epiplanktic.

Goniophara cymbaeformis and Modiolopsis sp.

Stanley (1972) considered that Modiomorphaceans were very similar to Modiolus which he showed to have an endobyssate life habitat. Both Goniophora and Modiolus show an elongate prosocline shell form with a

reduced anterior and an absence of ventral flattening. All these features are typical of an endobyssate life style (Stanley 1972). Levington & Bambach (1975) and Watkins (1978) also concluded that these genera were endobyssate. In life they would have been orientated with the sagittal plane vertical and the byssus would probably have emerged from the antero-ventral margin. Both Cherns (1977, p.259) and Stanley (1972, Fig. 28) have figured articulated specimens of Goniophora in the above orientation and both considered them to be in life position. Bambach (1971) recorded Grammysia obliqua in an identical orientation and from functional morphology and its relation to the enclosing sediment concluded it too was endobyssate, semi-infaunal, with the posterior margin above the substrate, allowing the inhalant and exhalant currents to freely flow in and out without fouling the shell. G. obliqua was considered to live with its radial groove parallel to bedding (Bambach 1971) and it seems that Goniophora lived with its keel parallel to bedding in a similar manner (Stanley 1972, Fig. 28). The ribbing of Goniophora would slow down burrowing but would act to stabilise the shell in the sediment (Stanley 1970; Trueman et al. 1966).

Cypricardinia planulata and C. subplanulata

Stanley (1972) noted that Cypricardinia was very like Modiolus in shell form and considered that like the latter genus it was endobyssate living partially buried in the sediment with its posterior margin above the surface to allow inhalant and exhalant currents to flow without fouling the shell with sediment; it lacked a pallial sinus. It had a byssus protruded from the antero ventro margin of the shell to anchor it. Since the valves are of similar convexity the shell presumably lived with the sagittal plane vertical. Although the strong concentric ribbing would have hindered the burrowing ability of Cypricardinia it would have served to anchor and stabilise this only semi-buried genus (Trueman et al., 1966; Stanley 1970).

Orthonota nasuta and Sanguinolites sp.

Both these taxa are elongate with coarse concentric growth lines. Stanley (1972) commented on the difficulty of assigning pholadomyacean species with elongate shapes to a free burrowing or endobyssate mode of life. Watkins (1978) considered Orthonota was endobyssate, however, Levington & Bambach (1975) thought it was an infaunal suspension feeder due to its Ensis like shape. Kauffman (1969) also considered such a shape to be an adaption for an infaunal mode of life. Dr. L. Marsh has kindly examined specimens of both taxa from my collections and concludes that both were slow shallow burrowers. The strong concentric ornamentation

would obviously have hindered burrowing but would have acted to stabilise and anchor the shell in the substrate (Trueman et al., 1966; Stanley 1970).

Paracyclus sp.

Like modern lucinids this taxon is thought to be a free burrowing suspension feeder. The smooth, slightly biconvex circular shape was well adapted to burrowing vertically downward (Stanley 1970). Living lucinids have a mucus tube with the foot to channel their inhalant current, allowing them to live at depth in the sediment (Stanley 1972).

Nuculites antiquus

Levington & Bambach (1975) compared recent deposit feeding bivalves to those found in the Silurian of Nova Scotia, they concluded from a detailed morphological examination that Nuculites was a siphonate deposit feeder (it possesses a pallial sinus) which probably burrowed up to a few centimetres below the sediment surface. Yonge (1939) concluded from functional anatomical studies that all bivalves of the order Nuculoida were deposit feeders. Stanley (1972) noted their tendency to occur in mudstones and from the close similarity in shell form between Palaeozoic and Recent taxa came to the same conclusions. Stanley (1970) considered the enlarged pedal region especially significant, since this indicates a large foot which he associated with rapid burrowing for efficient deposit feeding. Nuculoids show a smooth streamlined shell ideal for burrowing through sediment; this is necessary since they need to move to new food supplies constantly. As they are restricted to deposits with a fairly high organic content they are found most frequently in fine, muddy sediments deposited in quiet water, and only rarely in sands (Stanley 1970).

Praectenodonta ludensis

P. ludensis belongs to the family Ctenodontidae of the order Nuculoida. Kauffman (1969) considered that all members of the Ctenodontidae were infaunal. Stanley (1972) concluded that all taxa of the order Nuculoida were deposit feeders based on the functional anatomical studies of Yonge (1939), the tendency for them to occur in mudstones and the close similarity between Palaeozoic and Recent members of the order. From an examination of the morphology of Recent and Silurian deposit feeding bivalves Levington & Bambach (1975) concluded that Praectenodonta was a non-siphonate deposit feeder (it lacks a pallial sinus). The lack of siphons would have restricted it to the uppermost sediment. They considered that its heavy concentric ornamentation probably meant it was only a slow burrower. Trueman et al. (1966) and Stanley (1970) also noted that ribbing hindered burrowing but acted to stabilise and anchor the animal within the sediment, especially at the shallow depths this form probably occupied.

Plethomytilus mytilimeris

Stanley (1970, 1972) has argued that the mytiliform shape of ambonychiids such as Plethomytilus, with a reduced anterior region and a gross shell form similar to Mytilus is an adaption to an epibyssate life style, since the anterior reduction brings the byssal retractor muscles into a position more directly above the byssus where they can pull the ventral shell margin against the substratum with a strong direct force. This is vital for firm anchorage, especially in an epifaunal species. Stanley (1972) noted that many of the ambonychiids such as Plethomytilus had shells which were not as broadly based as the modern Mytilus which is more biconvex and shows a marked shift ventrally of the maximum shell width from midway along the dorso ventral axis (its position in most burrowing bivalves (Stanley 1970)). According to Stanley (1972) these adaptations in Mytilus were for strong anchorage of the shell to the substrate. However, as the ambonychiids are less broadly based than Mytilus they offer disruptive forces a larger mechanical advantage against the byssal apparatus. Stanley (1972) therefore suggested that the ambonychiids lived in less exposed habitats than recent epifaunal mytilids. The smaller size of the byssal retractors in ambonychiids, compared to mytilids, also indicates a less stable mode of life and therefore a probable preference for quieter conditions than modern mytilids (Stanley 1972). The equivalve nature of the shells indicates that attachment was such that the sagittal plane was near vertical.

Grammysia sp. A

Bambach (1971) from an examination of Grammysia obliqua, found in presumed life position, and a detailed investigation of its functional morphology concluded that it was endobyssate, living with the dorsal posterior region of the valves above the surface to allow the free flow of inhalant and exhalant currents without fouling the shell with sediment; it had no pallial sinus. Stanley (1972) however noted that other species of Grammysia were of different shapes which suggested they were probably free burrowing suspension feeders. Grammysia sp. A has been recognised, described and its functional morphology investigated in detail by L. Marsh (1976) in her Ph.D. thesis. However her work is still unpublished so that here it is referred to as Grammysia sp. A. She concluded that this species lived intertidally or possibly just subtidally and was a rapid shallow burrower in these high energy conditions (L. Marsh 1976; L. Marsh pers. comm. 1978). Since this species was a shallow burrower and lived in high energy environments, where exhumation from the sediment was common place during life, the ability for rapid burrowing was necessary for survival (L. Marsh 1976; Stanley 1972).

BRYOZOANS

Modern bryozoans are mainly marine forms, although they range from littoral to abyssal depths. They are commonest in shallow shelf seas (i.e. depths of generally less than 200 m) and few exist in the intertidal zone. Factors which influence the distribution of modern forms are temperature, the need for good water circulation (although too much turbulence, from waves for example, is unfavourable) and the presence of firm substrates for larval settlement. Some species of bryozoan are particularly adapted for life on one sort of plant or one type of shell and are therefore limited by the distribution of such substrates. Others are capable of anchoring themselves by rhizoid rootlets into soft sediments; some are commensals living on, for example, gastropod shells where they can survive successfully on a substrate which might otherwise lack attachment sites. Salinity is very important since it restricts almost all species to a marine environment; turbidity is also important since no forms are capable of tolerating anything but slow rates of deposition (Ryland 1970). From a study of modern forms it can be concluded that there is a very close relationship between bryozoan form and environment (Stach 1936; Lagaaij & Gautier 1965; Ryland 1970). The conclusions of these authors relevant to Lower Bringewoodian forms are given below.

Encrusting types (Ceramopora sp., Fistulipora sp., encrusting trepostomes and encrusting cystoporates)

Although Stach (1936) thought that encrusting bryozoans were largely typical of shallow nearshore environments, Ryland (1970, p.67) has shown that their distribution depends on the presence of a hard substrate more than anything else. Encrusting forms can be found on soft as well as hard substrates as long as the former has hard sites of attachment present (e.g. shells).

Erect and articulated (Ptylodictya lanceolata)

Since these colonies can bend Stach (1936) considered that they were adapted to nearshore, more turbulent environments. However Lagaaij & Gautier (1965) found that forms like this were able to stand slow silt deposition off the Rhône delta (although this excluded all other types of bryozoans) as they could attach to silty bottoms (with no attachment sites) by anchoring themselves with basal rootlets, their form being ideal for such environments since they lack horizontal surfaces on which smothering silt could accumulate. Dr. P. Taylor (pers. comm. 1978) considers that some P. lanceolata specimens may have been anchored in

soft sediment by rhizoids; it is therefore possible that these may have been able to withstand environments with slow silt deposition.

Vinculariiform (vinculariiform trepostome)

Stach (1936) and Ryland (1970) considered that such forms were ideal for quiet water, since only turbulence would quickly break up the delicate, brittle, erect and branching colonies. Lagaaij & Gautier (1965) confirmed this in their analysis of bryozoan distribution around the Rhône delta.

Dendroid (dendroid trepostome)

The thicker branches and stronger form are probably adaptations for slightly more turbulent water than that of the vinculariiform colonies (Stach 1936; Ryland 1970; Taylor, pers. comm. 1978).

GRAPTOLITES

Lapworth (1897) considered that graptoloids were epiplanktic, attached distally by their nemas to masses of floating weed comparable to the modern Sargassum. As Bulman (1955) noted this accounts for both the nema and the widespread distribution of graptolites, however he also drew attention to Ruedemann's discovery (1895 and many later references) of associations of rhabdosomes grouped around what appeared to be a central float, which suggested that some of the Graptoloidea may have had a truly planktic mode of existence. Kirk (1972) however, has suggested that synrhabdosomes may have functioned to anchor the rhabdosomes to the sea floor, but as Rickards (1975) pointed out the synrhabdosomes are found in an anaerobic black shale environment where they cannot possibly have lived and so must have lived above. Kozlowski (1949), Bulman (1964, 1970) and Rickards (1975), from a detailed study of synrhabdosomes, could only detect a mass of tangled nema and concluded that it was unlikely they constituted a primary buoyancy mechanism but probably represented associations for the purpose of sexual reproduction. Rickards (1975) from a detailed study of the nema of graptoloids concluded that it was unlikely they could function as attachment organs to foreign bodies. He therefore rejected the idea that graptoloids were epiplanktic and considered it far more likely that they possessed their own buoyancy system as proposed by Bulman (1964, 1970) and Kozlowski (1971). They suggested that graptoloids lived suspended below gas filled vacuolated tissue in the uppermost water layer (the neustron zone) and were therefore holoplanktic. In the more compact and less buoyant graptoloids vanes have been found which may have acted as supports for vacuolated extrathecal tissue. In the proportionately longer and more slender monograptids such structures are rare and therefore

it is presumed that the normal nema was quite capable of holding sufficient vacuolated tissue to support the colony in the neustron zone (Rickards 1975). Additional evidence for this idea comes from the discovery that the size of a bubble of oxygen sufficient to keep vane bearing graptoloids buoyant is similar in size to the vanes (Rickards 1975).

Kirk (1969, 1972, etc.) however, argues that graptoloid colonies had mobility as a result of the concerted activity of the zooids causing directional currents. She argued (Kirk 1969) that if graptoloids had lived at the surface amongst the waves then more colonies would have been broken than are found. However, Rickards (1975) notes that over half the colonies found <u>are</u> broken which in view of the quiet environment of preservation indicates that the life environment was turbulent. Bulman (in Kirk 1969) argued from the manner in which the ciliated lophophore currents are used by the living <u>Rhabdopleura</u> it was extremely unlikely that graptolites could have directed forcible currents. Bulman (1964) had noted the small zooid bulk compared to the relatively huge weight of the skeleton and for this reason (pers. comm. in Rickards 1975) rejected automobility. Many other objections to Kirk's hypothesis are given in the discussion of Kirk (1969) and in (Rickards(1975).

Berry & Boucot (1972), Erdtmann (1976) and Kaljo (1978) have all advanced the concept of bathymetrically arranged graptolite biocoenoses in the Llandovery of the U.K. and U.S.A., the Ordovician and the East Baltic Silurian respectively. However, Rickards (1975) has noted that the most common offshore species are those found rarely in the inshore (shallower) facies and that the inshore species tend to be the most robust taxa. It is therefore possible to explain such 'bathymetric' graptolite distributions in terms of selective preservation of the more robust forms in the agitated inshore environments with the more delicate forms being destroyed. Furthermore, Bulman (1964) has argued that the complex relations between compression of gas at depth and loss of buoyancy make it extremely unlikely that any colonial organism dependent on gas bubbles could maintain themselves at particular depths, or be anything other than surface living forms.

Bulman (1964) by plotting the distribution of graptolite species against the relevant palaeoequator derived from palaeomagnetic data convincingly demonstrated the equatorial nature of graptolites and suggested that temperature controlled their geographic distribution with the most abundant and diverse fauna in the tropical or warm temperate zone. Skevington (1974) also stressed the role of temperature in the control of graptolite distribution and maintained that the Ordovician Pacific and Atlantic graptolite provinces could be interpreted in terms of latitudinal climatic belts.

Watkins & Berry (1977) noted that graptolites are more abundant and their species diversity higher in the Ludlovian basinal area compared to the shelf. They noted that the distribution of modern zooplankton, where oceanic and coastal water masses meet, is such that zooplankton like foramanifera show a marked decline in density and diversity in a shorewards transect. They therefore explained the Ludlovian graptolite distribution in terms of different surface water masses existing over shelf and basin, the 'graptolitic water mass' over the basin containing a high density and diversity of graptolites while the 'shelf water mass' contained only a low density and diversity graptolite assemblage. They also considered that in the 'graptolitic water mass' large masses of Sargassum like algae floated on which a 'pelagic community' of bivalves and brachiopods lived. However, they failed to consider the selective preservation factor noted by Rickards (1975). The reduction in density of graptolites from the basin onto and over the shelf and their decrease in diversity over this transect too, may just be due to all the more fragile ones and many of the stronger ones being broken up in the more turbulent waters of the shelf.

CEPHALOPODS

Longicone orthocones were probably nektic and by comparison with modern cephalopods may have been predators and scavengers. Cyrtocones with a moderate conch curvature (e.g. 'Cyrtoceras' and Paraphragmites) were also probably nektic since moderate curvature would produce a stable orientation of the shell with the hyponome horizontal. However the mode of life of brevicones (such as Gomphoceras) is not as easy to deduce; in some the phragmacone is so small compared to the size of the animal that its weight must have kept the shell from becoming buoyant and they must have had a vagrant benthic mode of life. Other brevicones, however, with proportionately larger phragmacones were probably buoyant and therefore may have drifted or swum (Furnish & Glenister 1964).

Westermann (1973, 1977) argued that as the tensile strength of a curved membrane is directly proportional to the ratio of its thickness and radius of curvature, then by measuring the concave septa of fossil cephalapods the mechanical strength of the septum against implosion can be calculated and hence the depth to which the animal could go. The implosion depth of longicones varied from 50 m to 800 m and that of brevicones from 50 m to 250 m.

Denton (1974) noted that modern nautiloids live almost as far down as their implosion depth with only a low margin of safety so that

the implosion depth figures approximate the depth to which the animal may have ventured in life. Saunders & Wehman (1977) experimented on the implosion depth of the modern Nautilus and found adult shells imploded at pressures approximating to depths of 300 m to 700 m (although the figure for small, immature shells, could be as high as 1360 m) because of this wide range of implosion values they argued that the determination of depth ranges in fossil cephalopods required caution.

Watkins & Berry (1977) noted that one group of Ludlovian orthocones (mainly large and ornamented forms) were associated with the 'shelf' benthic communities, while another group (small unornamented forms) were located in basinal sediments, the overlap between the two groups being very small. They concluded that the 'shelf' forms (e.g. 'Cyrtoceras', Dawsonoceras, etc.) were nektobenthic with a predatory mode of life, while the basinal forms were nektic inhabiting the surface waters amongst the graptolites. Bulman (1964) had also noted that small smooth orthocones in the Upper Silurian were common associates of the graptolites and considered them to be epipelagic plankton.

GASTROPODS

Most marine forms are benthic and live in comparatively shallow water (although some live at abyssal depths and some have enormous depth ranges). Most gastropods are herbivores, carnivores or deposit feeders. Cocks & McKerrow (1978) have argued that since Silurian shells show no sign of attack by gastropods with rasping radulae it is likely they were scavengers or grazers and not predators. It is not uncommon for marine species to tolerate brackish water and live in estuaries, e.g. Littorina (Cox 1960).

Caenogastropoda

Living members of the Caenogastropods can cope with fine suspended sediment and therefore live in environments of soft sediments (Peel 1978). Loxonemids probably lived on soft sediments on shallow water platforms as microherbivores, living off algal covered surfaces (Peel 1978). They are therefore thought to have been epifaunal deposit feeders. Linsley (1978) argued that with such high spired shells the centre of gravity is so high that it is no longer practical for the animal to hold the shell over its body and so it drags the shell behind itself. Obviously such forms are slow movers; they do not move often and when they do it is very laboured. The presence of L. obsoletum up to the base of the Downtonian in the Welsh Borders, which probably indicates the change from marine to non-marine deposition, indicates its tolerance for shallow water, possibly not fully saline conditions.

Archaeogastropoda

Recent members of the Archaeogastropoda are generally restricted to hard bottoms and clean water since they are unable to cope with fine suspended sediment. However, their life style may not have always been so restricted because recent members of the order may have a narrower range of habitats than their Palaeozoic ancestors due to competition from the highly successful caenogastropods which have come to dominance since the Lower Palaeozoic (Peel 1978).

Liospira has been interpreted as an epifaunal deposit feeder or foliage browser by Peel (1978). The tangential aperture (the aperture plane is tangential to the body whorl) indicates that the shell was balanced on the cephalopedal mass allowing the animal to crawl about continuously, and could quickly protect itself by clamping the shell over the body (Linsley 1977; Linsley et al., 1978). The low spired nature of the shell probably meant that these shells were fairly fast movers, by gastropod standards (Linsley 1978).

Bembexia is very similar to trochiform pleurotomariaceans interpreted by Peel (1978) as epifaunal deposit feeders. The tangential aperture indicates that the shell was carried on the cephalopedal mass, allowing the animal to crawl about continuously; the snail could obtain protection merely by clamping the shell over the cephalopedal mass (Linsley 1977; Linsley et al., 1978). The medium spired nature of the shell means the centre of gravity was fairly high and therefore they were probably slow movers (Linsley 1978).

Poleumita has a radial aperture (the aperture plane passes through the axis of coiling). Gastropods with a radial aperture do not carry their shells above their boides; instead their shell is allowed to rest on the substrate and they rarely locomote; when they do the animal drags the shell along. Such shell draggers are the slowest moving gastropods and as all modern forms displaying this degree of immobility are filter feeders (Linsley 1978), it is considered Poleumita was too.

TRILOBITES

Most trilobites were deposit feeders, scavengers or active predators (Bergström 1973).

Dalmanites myops

Bergström (1973) noted that dalmanitids were rarely found enrolled, although examples are known. He suggested that trilobites with large eyes, reduced enrolment capabilities and a wide axis (indicating the possible presence of powerful muscles at the appendage bases) indicated

a swimming (probably nektobenthic) mode of life. However no work has been done on the mode of life of dalmanitids. Cocks & McKerrow (1978) considered the large eyes of this species were adaptations for life in deep water conditions at 'Visbyella community' depth.

Proetus astringens and P. obconicus

Fortey & Owens (1975) considered that proetids lived in shallow water, sometimes 'reef' environments. They also noted that proetids appeared to be more abundant in limestones, although they were not confined to this lithology. Cherns (1977) noted that Lower Leintwardinian proetids were most abundant in the distal shelf facies. They therefore appear to be confined to 'shelf' environments.

Encrinurus rosensteinae and E. stubblefield

Encrinurids probably lived partially buried in the sediment. The tuberculate cephalon may have acted as camouflage and the stalked eyes would have allowed them to see while most of their body was buried under a thin film of sediment. They may therefore have been predatory (Tripp 1977, pers. comm.).

Calymene lawsoni and Calymene sp.

Bergström (1973) suggested that calymenids were probably burrowers in soft sediment. He based these conclusions on Flexicalymene which he related to some Cruziana trails and the reported occurrence of this genus in burrows. However, Dr. Derek Siveter (pers. comm. 1978) warns against generalisation although he considers all members of the class were benthic or nektobenthic and confined to shelf areas. Cherns (1977) noted that C. lawsoni was most abundant in the canyon heads of the Lower Leintwardinian and suggested this distribution may reflect a preference for more sheltered conditions.

Homalonotids

Bergström (1973) suggested that the wide axis (which indicates plenty of room for powerful muscles at the appendage bases, essential for burrowers), the smooth exoskeleton (which would reduce friction in burrowing) and small eyes of homalonotids were all adaptations for burrowing in soft sediment. Sdzuy (1957) had already suggested a burrowing mode of life for this group. Boucot (1975) noted the tendency of homalonotids to be common in nearshore sediments, suggesting they were well adapted to such a proximal environment.

CORALS

By analogy with living coelentrates these are interpreted as forms attached, at least initially, to the substrate and feeding either as

passive predators, the large polyp bearing corals, or as suspension feeders, the small polyp bearing tabulates (Walker & Laporte 1970).

All modern reef building corals live in warm, shallow, clear seas in tropical or subtropical areas, although some solitary and rare colonial forms are found in cold water and may live at considerable depths. By analogy it is possible to assume that ancient anthozoan 'reefs' may have lived in the same conditions as modern reef builders, though this may be incorrect. However, it is notable that when they are found the associated sediments usually do suggest shallow and clear waters (Shrock & Twenhofel 1953).

Newall (1966) found that compound corals were flatter in Upper Bringewoodian rocks he considered were deposited in more turbulent conditions and suggested this may be because dome shapes would be more easily overturned in such conditions. Abbott (1975) noted that compound corals in recent Florida reefs are smooth under rapidly flowing water, but mamillated in quiet conditions; he considered that Wenlockian Favosites and Heliolites became mamilated in rocks he inferred to have been deposited under quiet conditions. Abbott (1975) and Gill & Coates (1977) suggested that some spherical corals, with concentric growth laminae and no epithecae may have been mobile, rolling along the sediment surface either in response to currents or the beating of the polyps tentacles. Gill & Coates (1977) proposed such forms were ideally adapted for environments with high deposition rates in which sedentory forms may have been buried.

Corals appear to require clear well circulated water which would bring in food and oxygen. Warm, clear, shallow seas were probably needed by reef builders. The shape of corals is dependent on the environment.

OSTRACODS

Modern forms are mostly herbiverous, mainly grazing on algae, while others are scavengers on decaying vegetation or small animals (Morkhoven 1962). Whatley & Wall (1975) noted that algae were extremely important in influencing the distribution of modern ostracods in Cardigan Bay. Martinsson (1962) considered that beyrichiids were benthic but because they are found in a large range of facies he suggested they lived to a large extent on algal vegetation. Cherns (1977) considered that non-palaeocopes were also benthic. She noted that ostracods and A. grayi commonly occurred together as thin seams in the basinal sediments of the Lower Leintwardinian and suggested they may have been attached to shelf algal vegetation which was uprooted and carried into the basin

with these shells still attached. Both beyrichiids and non-palaeocope ostracods may have been strongly influenced by algal vegetation.

CRINOIDS

Cain (1968) considered that stalked crinoids were probably mainly shallow water dwellers, in the past, although at the present day this niche is filled by free swimming crinoids, which arose in the Mesozoic, while stalked forms are confined to deeper water. Cain noted that crinoids both today and in the past occur on a wide range of substrates and suggested that sediment composition or grain size were not limiting factors but rather that the requirement was for an abundance of suspended organic matter since they are filter feeders.

Watkins & Hurst (1977) examined crinoids from the Wenlock Limestone at Dudley and reviewed their occurrence in other Silurian strata. They concluded that favourable conditions for crinoid growth were relatively shallow, clean and well circulated water, substrates with much skeletal material and slow sedimentation rates. Active sedimentation in terrigenous soft bottom environments was considered to limit the diversity and abundance of crinoids.

Shallow, clean, well circulated water with abundant suspended organic matter appears to provide the optimal conditions for crinoids.

TENTACULITIDS

Fisher (1962) argued that tentaculitids were nektobenthic scavengers in fairly agitated waters, since the rings about the conch were considered to be strengthening features. Thayer (1974) and Walker & Laporte (1970) considered tentaculitids were vagile deposit feeding benthos. Blind (1969) considered that the microstructure and morphology of tentaculitids indicated a close resemblance to cephalopods. He suggested from the evidence of geopetal infills that the adults lived attached to the substrate by their apex and were therefore presumably sessile suspension feeders. Further support for this latter idea is that epizoan hosts, presumably growing positive phototropically are found parallel to the length of the shell and growing from the apex towards the aperture of the shell (Blind 1970). Hurst & Hewitt (1977) examined Caradoc tentaculitids and noted a molluscan shell structure, which agreed with the work of Blind. From a consideration of shell morphology they suggested an infaunal, benthic, suspension feeding mode of life was most likely. Recently Towe (1978) has suggested that tentaculitid shell morphology and mineralogy indicates they were possibly specialised articulate brachiopods or calcified phoronid tubes. In conclusion,

whatever their affinity, tentaculitids were probably benthic suspension feeders.

ANNELIDA

Cornulitids are calcareous worm tubes which fix the curved end of their tube to the host, usually gastropods, bryozoans or brachiopods. However gerontic ones may often have lived free with the initial tip missing, and it is presumed to have broken off (Fisher 1962).

Keilorites was a worm which lined the burrow in which it lived with a membranous material which can be preserved (Howell 1962).

CHAPTER 3

THE SHELF-SECTIONS, SEDIMENTOLOGY AND FAUNAS

SETTING

The calcareous siltstones of the Lower Bringewoodian shelf yield a fauna of abundant and diverse brachiopods (including many strophomenids) and are sandwiched between a) the low density, low diversity fauna of the less calcareous, flaggy Upper Elton Beds whose fauna is very restricted and is dominantly composed of graptolites, orthocones and the brachiopod S. ludloviensis and b) the more calcareous silty, nodular limestone facies of the Upper Bringewood Beds with their brachiopod-coral fauna.

The areal extent of the shelf facies during Lower Bringewoodian times is shown in Fig. 1.1. The calcareous siltstones of the Lower Bringewood Beds, the strophomenid siltstone facies of Holland & Lawson (1963), occupied the entire shelf area from just west of Aymestrey and Leintwardine to the farthest north-east (South Staffordshire) and south-east (Brookend borehole) they are known. In this area they are only recorded as being absent from the Gorsley region (Lawson 1954). The overall thinning of shelf isopach values (Fig. 1.2) to the east and south-east was considered by Holland & Lawson (1963, p.280) and Ziegler (1970) to indicate the probable approach to a shoreline (The 'Midland Block').

The exact position of the shelf edge is difficult to ascertain due to the lack of exposure between definite shelf and basin facies; however, the distance between clear examples of each is not great (a few kilometres) and therefore the transition between the two must be quite rapid. In Lower Bringewoodian times the shelf edge must have lain somewhere between Knill (with a basin facies and fauna) and Aymestrey (with a shelf facies and fauna) and run north between the shelf Wenlock Edge area and the basin area around Bishops Castle. Its inferred position is shown in Fig. 1.1 and is very similar to the line chosen by Holland & Lawson (1963, Fig. 5).

This line is very close to the line of the Church Stretton Fault, as Bailey (1964, 1969), Ziegler (1970), R. Marsh (1976), Bailey & Woodcock (1976) and Watkins (1979) have noted, see also Fig. 1.1. However, as Holland & Lawson (1963) have correctly noted, basinal facies and faunas do occur in outcrops up to a few kilometres east of the fault. These deposits, however, do contain slumps (e.g. the section at Knill, which lies 1 km to the east of the fault) and therefore must have lain on the

palaeoslope, so that the palaeoslope lay across the Church Stretton Fault complex. It will be argued later (p.100) that the coincidence of a major crustal feature (known to have been active previously) and a rapid transition from a shallow water 'shelf sea' area in the east to a contemporaneous subsiding basinal area in the west, involving a huge increase in the thickness of deposits laterally over a small distance strongly suggests that this eastern margin of the basin was fault controlled.

RECOGNITION OF THE LOWER BRINGEWOOD BEDS

The recognition of the Lower Bringewood Beds on both lithological and faunal criteria, as used in this study, is based on their description from the type area (Ludlow) by Holland et al. (1963). From the following descriptions of the 9 shelf sections examined it will become obvious that the Lower Bringewood Beds as defined below are recognisable over the whole shelf area. Although in both the Lower Bringewoodian and the underlying and overlying beds the abundance of various faunal elements and, to a lesser extent, lithology change laterally across the shelf.

Although the boundaries between the Lower Bringewood Beds, the underlying Upper Elton Beds and the overlying Upper Bringewood Beds are to some extent transitional the changes are rapid and it is possible to pick horizons in the Ludlovian succession where a Lower Bringewoodian fauna and lithology becomes established or disappears. The faunal and lithological changes always occur together.

The base of the Lower Bringewoodian is taken where thicker and more irregularly bedded, occasionally nodular, calcareous siltstones supercede the well developed flaggy bedded, siltstones of the Upper Elton Beds. Highly fossiliferous limestone beds (coquinas) become an increasingly common feature of the Lower Bringewood Beds with increasing distance from the shelf edge but are never more than very rare in the Upper Elton Beds and may therefore, when they occur, be used as an aid in establishing the boundary between these divisions e.g. Shergold & Shirley (1968) and White (pers. comm. 1978). The Lower Bringewood Beds also show a marked faunal contrast to the Upper Elton Beds. The latter have a relatively low diversity, low density fauna in which the dominant forms are usually S. ludloviensis, orthocones and graptolites. The onset of the Lower Bringewoodian is denoted by a marked decrease in the abundance of graptolites and orthocones and the appearance of many large brachiopod species (including many strophomenids) e.g. M. cf. lepisma,

L. filosa, Shaleria sp. nov., C. pecten, L. depressa, A. funiculata, G. lata, S. wilsoni, A. reticularis, M. nucula, H. elegans and S. euglypha which are absent or extremely rare in the Upper Elton Beds (although the latter species occurs fairly commonly in the Upper Eltonian of the Brookend borehole). With the influx of these new species the faunal density and diversity rises. Most of the typical Bringewoodian fossils are "Wenlockian species returning with the change to shallow water and calcareous conditions" (Holland et al. 1963, p.112).

The base of the Upper Bringewoodian is taken at the change in lithology from irregularly and thickly bedded calcareous siltstones (Lower Bringewoodian) to irregularly bedded, silty, nodular limestones, which have thin shale bands every few metres (i.e. the 'Aymestry Limestone') in all but two sections (Bengry Track and Brookend borehole) where although the Upper Bringewood Beds are far more calcareous than the Lower Bringewood Beds, with abundant calcareous nodules, they cannot be considered to be a silty limestone. The fauna also changes at the base of the Upper Bringewoodian; although it is similar to the Lower Bringewoodian fauna, many species typical of the latter division e.g. L. filosa, S. ludloviensis, C. pecten, M. cf. lepisma and Shaleria sp. nov. are missing or rare, while A. reticularis and S. euglypha are common together with corals which have increased in abundance from the lower division. K. knightii is found almost exclusively in the Upper Bringewood Beds with rare occurrences in the Lower Bringewood Beds at Ludlow and Leintwardine, recorded here for the first time. Bands with abundant K. knightii or compound corals are a common and distinguishing feature of the Upper Bringewood Beds both at, and to the west of Ludlow.

DIACHRONISM OF THE LOWER BRINGEWOOD BEDS?

It is possible that the Ludlow divisions are diachronous, since the criteria for recognising them are largely based on lithology and assemblages of benthic fossils, both of which are highly influenced by the environmental conditions present at any one time and which may vary from place to place. However, the Ludlow divisions do show a remarkable parallelism with the graptolite zones within the Ludlow (Lawson 1973a; Rickards in Ziegler et al. 1974; Lawson 1975) which indicates that marked diachronism is very unlikely. Lawson (1975) has suggested the reason that diachronism of the Ludlow divisions is not easily demonstrated is because over the whole shelf area fairly uniform conditions may have persisted at any one time, he concluded that correlation of the Ludlow divisions over the shelf area appears to be sound.

During this study a careful search for graptolites was made and these were kindly identified by Dr. R.B. Rickards. S. clunensis is recorded from shelf facies Lower Bringewood Beds for the first time.

From the River Onny section only P. tumescens was recorded from the Lower Bringewood Beds indicating a mid scanicus Zone to incipiens Zone time span (Rickards 1976). Graptolite assemblages found in the Lower Bringewood Beds of Woodbury (S. clunensis and S. chimaera semispinosus), Ludlow (S. clunensis) and Leintwardine (P. tumescens, S. incipiens and S. clunensis) all indicate a mid scanicus Zone to mid incipiens Zone range (Rickards 1976). At Aymestrey the highest Lower Bringewoodian contains S. chimaera salweyi and the highest Eltonian contains S. clunensis (Lawson 1973a, p.261) so that here the Lower Bringewoodian can be no older than mid scanicus Zone and yet no younger than topmost scanicus Zone (Rickards 1976).

The graptolites recorded therefore indicate no diachronism of the Lower Bringewoodian and (from the Aymestrey results) indicate this division must lie within the upper part of the scanicus Zone. Watkins & Berry (1977) list P. tumescens and S. cf. chimaera salweyi from the Bringewoodian of the shelf which also indicates an upper scanicus Zone age. An alternative explanation is that the range of S.c. salweyi may extend into the incipiens Zone; if this were so then the Lower Bringewood Beds would belong to the lower part of this Zone as has been suggested by Holland et al. (1963) and Cocks et al. (1971). The latter idea is favoured by the author. Holland & Palmer in 1974 extended the range of Bohemograptus to make it the youngest graptoloid in Britain.

Diachronism of the Lower Bringewood Beds is also considered unlikely on palynological evidence. Palynological assemblages analysed by Dr. Dorning (pers. comm. 1978) from the Bengry Track (Aymestrey) and the Brookend borehole, two of the most difficult places to fix the upper and lower limits of the Lower Bringewood Beds, support the boundary positions chosen on lithological and faunal criteria. These results are considered especially significant because of the large distance between these sections; Brookend being the most south-easterly and Aymestrey almost the most north-westerly locality from which Lower Bringewoodian, of the shelf facies, are known.

SHELF SECTIONS

Each of the sections through the Lower Bringewood Beds examined during this study is considered in turn. The first one discussed

(Aymestrey) is that considered to be nearest the shelf edge, subsequent sections are considered with increasing distance from the shelf edge.

As prose descriptions for faunal variation tend to be lengthy, charts were compiled on which the relative abundance of each species present in a section, the lithological variation up the succession, the position of samples collected and the density and diversity of each sample are clearly and accurately shown. From these charts (Figs. 3.2 to 3.10) faunal variation can be examined in a quantitative way. A key to symbols used in these charts is given in Fig. 3.1.

As each section is considered in turn its geographic location, position of samples from it and the criteria used for establishing the upper and lower limits of the Lower Bringewood Beds are discussed.

i) Aymestrey

The area around Aymestrey was mapped by Lawson (1973a). The only continuous section through the complete Lower Bringewoodian succession was the mechanically excavated Bengry Track which commenced at SO 41756567 and ran south-east from here. For the first 25 m along the track Upper Elton Beds were exposed, from 25 m to 106 m along the track a thickness of 21 m of Lower Bringewood Beds were continuously exposed, beyond 106 m (to 150 m) Upper Bringewood Beds were exposed (Lawson 1973a, Fig. 3 and p.261). However the bank of exposure along this track has now collapsed and it is entirely overgrown. Fortunately when Dr. Lawson examined the track he sampled in a similar method to that used here (except he sampled 0.9 m of section at a time (Lawson pers. comm. 1977) compared with 0.6 m in this study) so the results are comparable. Lawson's collections are now housed at I.G.S. (London) and it is here they were examined (by kind permission of Dr. D. White). The results of the present examination are given in Fig. 3.2.

The positions of the boundaries between the Lower Bringewood Beds, the overlying Upper Bringewood Beds and the underlying Upper Elton Beds are taken at the same position in the succession where Lawson (1973a) established them and are clearly defined on both lithological and faunal criteria.

The boundary between the Upper Elton Beds and the Lower Bringewood Beds is taken at the base of sample A6. Samples A1 to A5 show a typical Upper Elton Bed lithology of well developed flaggy (average 1 cm thick) siltstones. These beds contain a restricted low diversity fauna. Abundant S. ludloviensis is typical of topmost Upper Eltonian but the absence of graptolites is puzzling, since these fossils are normally so

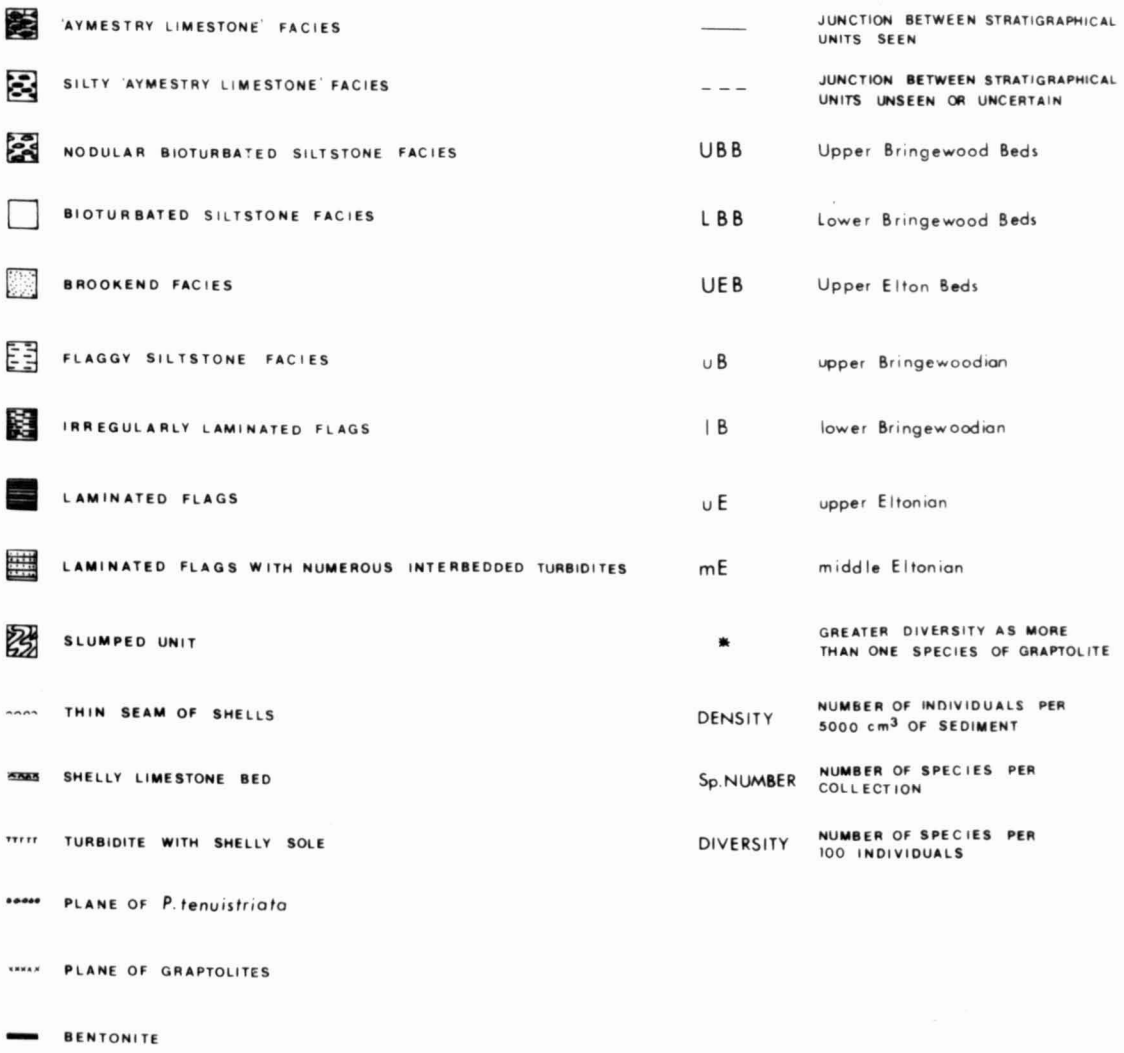


Fig. 3.1 Key to symbols used in Figs. 3.2 to 3.10 and 4.2 to 4.6

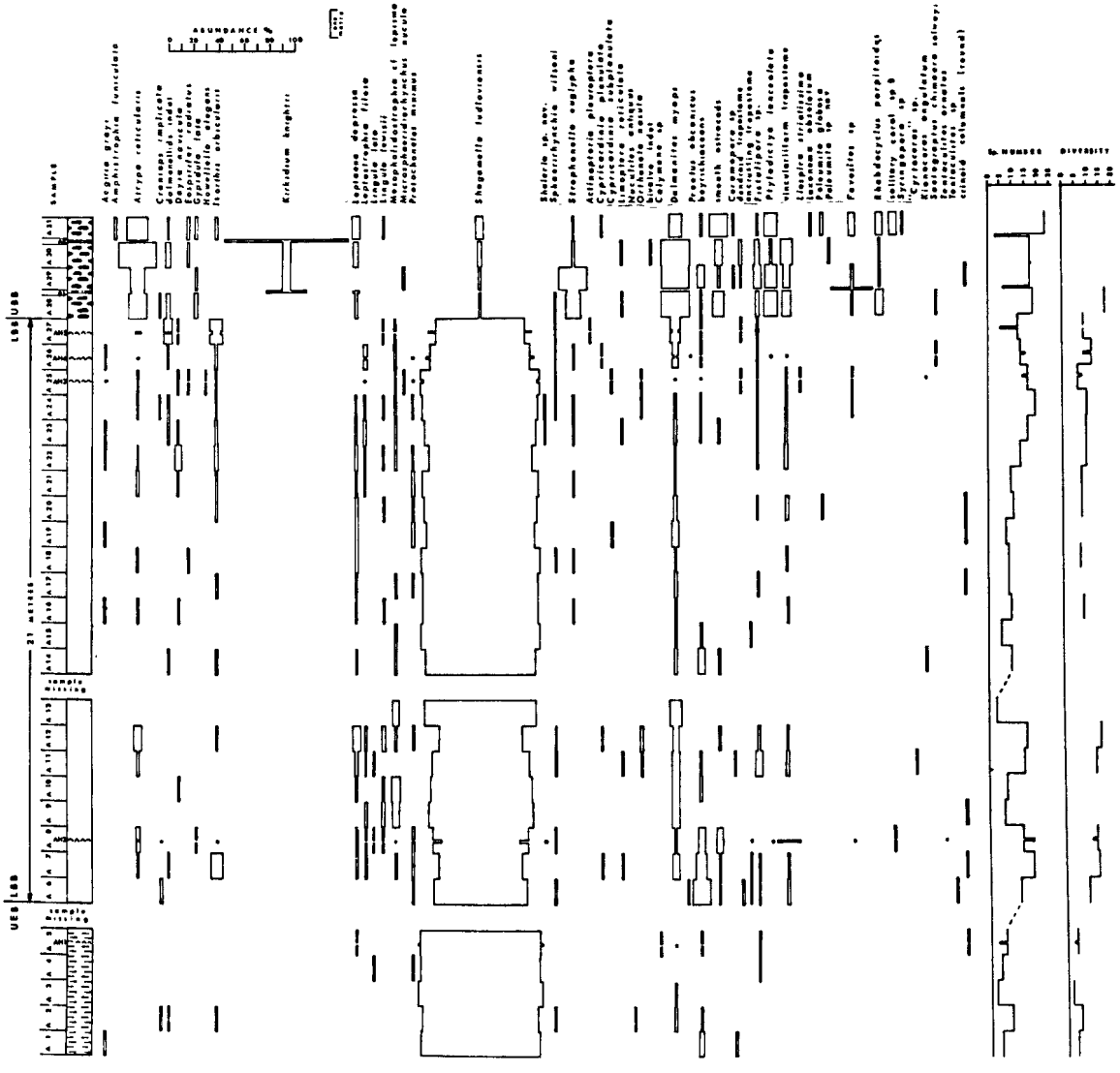


Fig. 3.2 The Lower Bringewoodian succession and fauna at Aymestrey (Bengry Track)

characteristic of this division, especially this far west. One sample rich in graptolites (S. clunensis) was, however, found by Lawson (1973a, p.261) in typical Upper Elton Bed lithology (this sample, between A5 and A6, is missing from the I.G.S. collection and is in the Sedgwick Museum (Lawson pers. comm. 1977)). Above the base of sample A6 the lithology is of thicker bedded (3 to 4 cm), more calcareous and irregularly bedded siltstones typical of the Lower Bridgewoodian. This lithological change is accompanied by the appearance of typical Lower Bringewoodian forms such as M. cf. lepisma, L. filosa, Shaleria sp. nov., S. euglypha etc. and an increase in fossil density and diversity. S. ludloviensis however remains the dominant species throughout the Lower Bringewood Beds.

The Lower Bringewood Bed - Upper Bringewood Bed junction can be placed on lithological and faunal criteria between samples A27 and A28. Above A27 the beds are more nodular and calcareous than the Lower Bringewood Beds; they also contain much shell debris and occasional cross bedding suggesting an increase in current activity. Therefore although the Upper Bringewood Beds of this area are not of the typical Aymestry Limestone lithology (as noted by Lawson 1973a) their junction with the Lower Bringewoodian can still be defined on lithological criteria. A marked faunal change is also obvious at this junction, the sudden decrease in abundance of S. ludloviensis and the disappearance of characteristic Lower Bringewoodian species e.g. M. cf. lepisma, Shaleria sp. nov. and L. filosa coincides with an increase of A. reticularis, S. euglypha, D. myops, corals, bryozoans and smooth ostracods. The presence of a Kirkidium band at AK, which Lawson (1973a, p.261) correlated with one in definite Aymestry Limestone facies Upper Bringewoodian exposed in a quarry some 0.4 Km to the east, and the common occurrence of Kirkidium in these more calcareous beds strengthens the argument that these strata are Upper Bringewoodian.

Sample AL is from a 7 cm thick bed of definite Aymestry Limestone lithology within the Upper Bringewoodian with Favosites sp., S. euglypha, A. reticularis and K. knightii in about equal proportions. Samples AH 1 to AH 5 are all from thin (1 to 2 shells thick) seams of shells in which faunal densities are very high compared to the surrounding sediment, suggesting shells have been concentrated into these bands in some way. In faunal composition they are similar to the beds above and below them, indicating limited transport, if any.

ii) Leintwardine

The area around Leintwardine was mapped by Whitaker (1962).

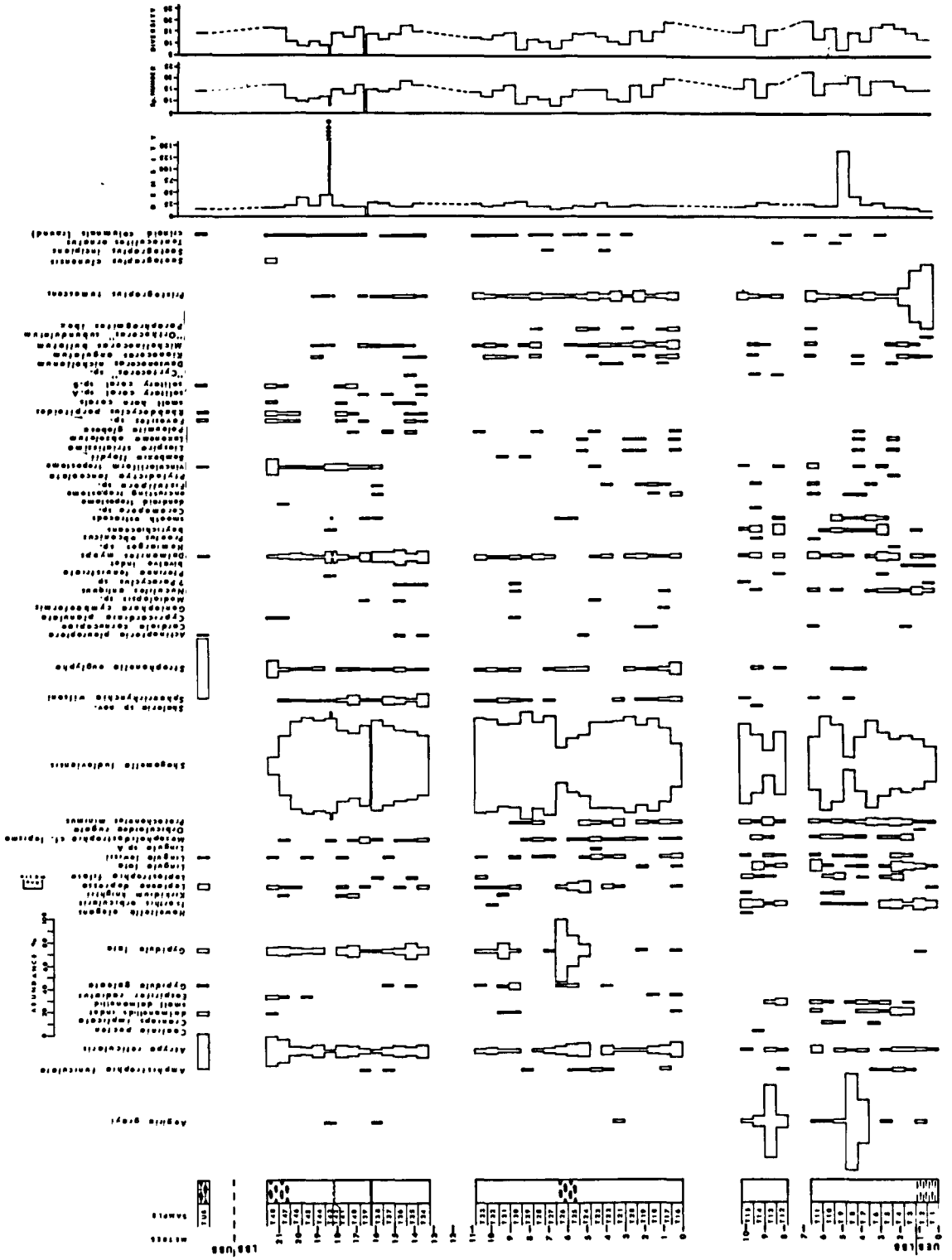


Fig. 3.3 The Lower Bringewoodian succession and fauna at Leintwardine

The sections examined in the present study (Fig. 3.3), which expose almost the entire Lower Bringewoodian succession, lie approximately 1.5 km north-east of Leintwardine village.

The uppermost Eltonian and the lower Lower Bringewood Beds were examined in a small quarry at SO 41097527 where 6.6 m of strata are exposed and samples T1 to T11 were collected. Although Whitaker (1962) assigned all the rocks in this quarry to the Lower Bringewood Beds and mapped the Upper Eltonian-Lower Bringewoodian boundary as passing some 10 m to the south-west of this quarry (op.cit., Fig. 3) detailed examination by the author has revealed that, in fact, the lowest 1.2 m of strata in this quarry (samples T1 and T2) belong to the Upper Elton Beds and therefore their junction with the Lower Bringewood Beds is exposed here. The Upper Eltonian in this quarry are flaggy (1 to 2 cm thick) siltstones although they are not quite so regularly flaggy as usual, this is attributed to their proximity to the Lower Bringewoodian. The fauna of these beds is typical of the Upper Eltonian with abundant P. tumescens and S. ludloviensis and a lack of characteristic Lower Bringewoodian forms such as M. cf. lepisma, L. filosa, S. euglypha etc. which appear in sample T3 (and above). The base of T3 is therefore taken as the base of the Lower Bringewoodian on faunal grounds. However, the boundary can be placed here on lithological criteria too, as above the base of T3 the lithology is of more irregular and thicker (4 to 6 cm) bedded calcareous siltstones, with occasional calcareous nodules which may occur in bands. This is the typical lithology of most of the Lower Bringewood Beds.

After a gap in the exposure, which is estimated to represent 1.2 m of strata, the section continues (over a track) in a cutting approximately 30 m due south of the uppermost beds exposed in the quarry. Here a further 2.4 m of Lower Bringewood Beds were examined and samples T12 to T15 were collected.

Lower Bringewood Beds from higher in the sequence were examined in an almost continuous road section along the A 4113. Between the lowest beds in this section, at SO 41367522, and the end of the exposure at SO 41607531 samples T16 to T48 were collected. Altogether 21.6 m of strata are represented in this section, with only 2.4 m of this unexposed near the Old Lime Kiln (SO 41487532). Whitaker (1962) in his map of the area shows a fault passing through this gap and a further fault cutting through the section, 30 m south-west of this. These faults are necessary further north to explain outcrop patterns but it

is suggested they may die out before reaching the road section since no evidence of faulting was seen. The highest beds of this section (samples T47 and T48) are very nodular and more calcareous; they contain a fauna which shows a decrease in S. ludloviensis and an increase in both A. reticularis and S. euglypha, suggesting the approach of the Upper Bringewood Beds. This is confirmed by the fact that 10 m due north of this last Lower Bringewoodian exposure the Upper Bringewood Beds are seen in the western Mocktree Quarry. A sample (TUB) was collected from the lowest 0.6 m of exposure. It contained a fauna dominated by A. reticularis and S. euglypha in a typical Aymestry Limestone lithology of the Upper Bringewood Beds, which is an extremely hard silty limestone with abundant calcareous nodules distributed throughout it. Bands of fossils rich in Kirkidium or corals and stromatoporoids were also noted but not collected. Newall (1966) in his thesis on the palaeoecology of the Aymestry Limestone reviewed this faunal distribution and his conclusions are discussed later.

Assuming that the last sample (T48) in the road section is in fact from the highest Lower Bringewoodian (and it may well be) and that neither of the sections is faulted (and there is no evidence that they are) then samples T3 to T15 come from the lowest 9.0 m of the Lower Bringewood Beds and samples T16 to T48 come from the uppermost 21.6 m, a total thickness of 30.6 m. Whitaker (1962) estimates the maximum thickness of the Lower Bringewood Beds in the Leintwardine area at 120 feet (op. cit., p.325) i.e. 36.6 m, and therefore the gap between the 2 sections (i.e. samples T15 and T16) may be only 6.0 m.

A thin shell seam with many fossils packed together occurs at T42 and is identical to those at Aymestrey. A 4 cm thick pale grey clay, which is totally unfossiliferous, occurs between samples T38 and T39 and is interpreted as a bentonite.

As at Aymestrey S. ludloviensis dominates the fauna throughout the Lower Bringewoodian except in samples T47 and T48 (already discussed), T26 and T25 where a more calcareous and nodular lithology occurs and G. lata becomes abundant and T13, T8 and T7 where A. grayi is abundant, but no change in lithology is seen.

iii) River Onny

This area was mapped as part of the Wenlock Edge region studied by Shergold (1967) and Shergold & Shirley (1968). Results of the present investigation of this section are given below and in Fig. 3.4.

The lower Upper Elton Beds are exposed in the river bank at

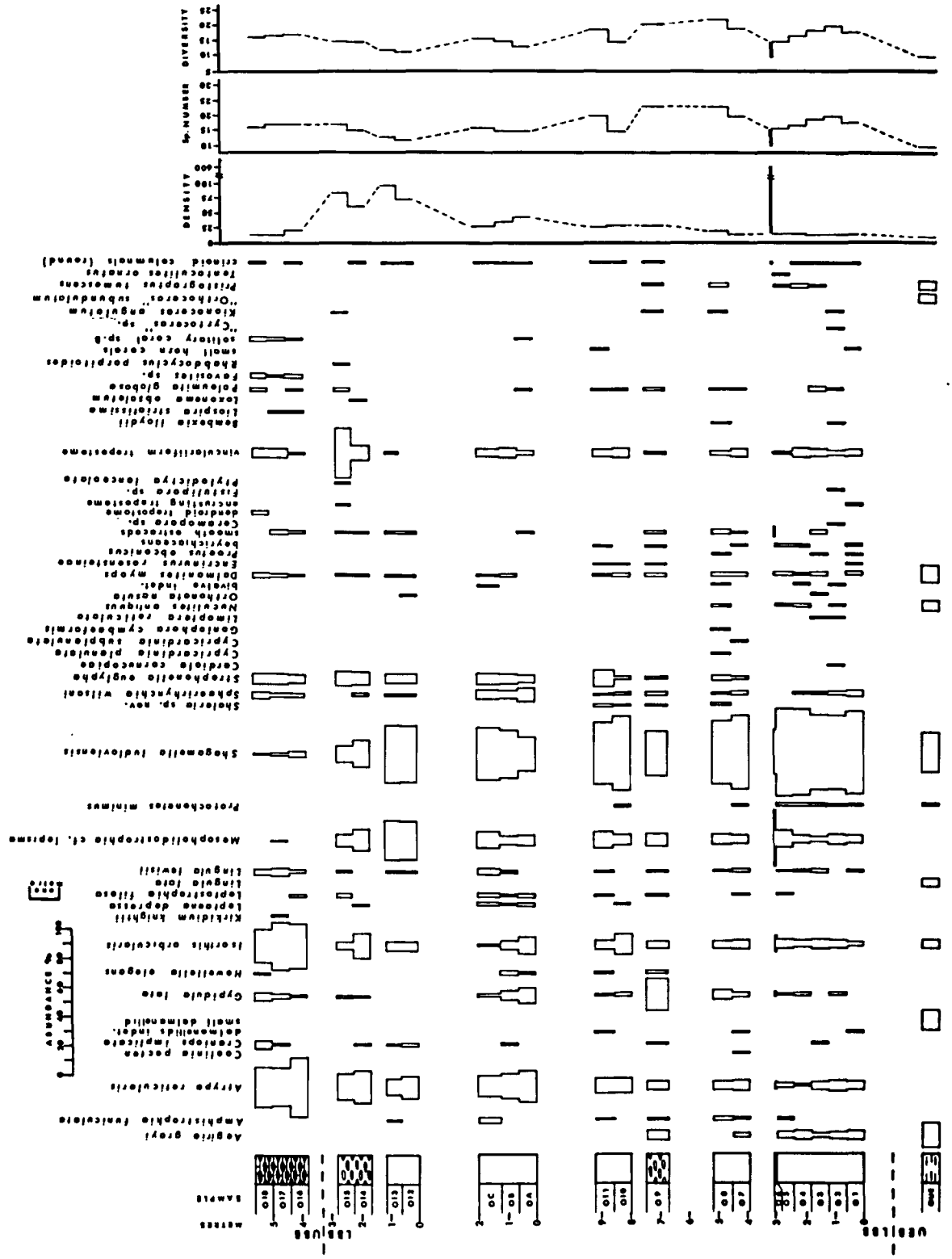


Fig. 3.4 The Lower Bringewoodian succession and fauna in the River Onny Valley

SO 44808088 and a 0.60 m thick sample (OUE) was collected. The characteristic flaggy (1 cm thick) bedding of the Upper Elton Beds is well displayed, graptolites are not as abundant as might be expected and the fauna is dominated by S. ludloviensis. The fauna is, however, low in density and diversity compared to the Lower Bringewoodian and lacks any fossils characteristic of this division. The uppermost Upper Elton Beds and the lower Lower Bringewood Beds are not exposed in this section.

The first exposure of the Lower Bringewood Beds occurs between SO 44358042 and SO 44408036 in a now quite overgrown roadside section along the A49. A total of 9.23 m of beds are represented (including 3 gaps which total 2.80 m) and samples 01 to 011 were collected. These beds are typically Lower Bringewoodian in lithology (irregularly and thickly (4 to 6 cm) bedded calcareous siltstones with calcareous nodules) and fauna (dominated by S. ludloviensis but distinctly Lower Bringewoodian with combinations such as A. funiculata, L. filosa, M. cf. lepisma, Shaleria sp. nov., S. euglypha etc.). The only exception is sample 09 which comes from more nodular and calcareous beds which show a marked decrease in S. ludloviensis and a rise in the abundance of G. lata. Sample 06 is from a 1.5 cm thick shell bed which shows a high faunal density compared to sediments above and below and is very similar to those found at Leintwardine and Aymestrey.

South of SO 44408036, strata are exposed in the river, however simple geometric constructions based on measurements in the field reveal that these beds are at the same stratigraphic level to those examined in the road section above.

The next beds to occur higher in the Lower Bringewoodian succession are by the riverside at SO 44498025. Geometric construction reveals that the lowermost of these beds must be some 7 m above the last strata seen in the road. Altogether 1.98 m of beds are seen and samples OA to OC were collected. The lithology of the beds is as before but S. ludloviensis is less abundant while A. reticularis is becoming more so.

The next exposures (following an estimated 17 m gap) of Lower Bringewood Beds occur a few metres north and south of the footbridge across the river at SO 40608014. Here 2.78 m of beds were measured (including a 0.5 m gap) and collections 012 to 015 were obtained.

Samples 014 and 015 are from the more calcareous and nodular Lower Bringewoodian lithology. In these beds the abundance of

A. reticularis and I. orbicularis increases while that of M. cf. lepisma and S. ludloviensis declines. All of those factors suggest the approach of the Upper Bringewoodian. These beds yield large quantities of vinculariiform trepostome bryozoans. This is the so-called 'bryozoan bed' of Shergold (1967) and Shergold & Shirley (1968) whose base they took to mark the Lower-Upper Bringewoodian junction. It is, however, just a series of beds in which bryozoa are commoner than is usual in the Bringewoodian and not a bed composed almost exclusively of bryozoa, as the descriptions given by the above authors imply.

After a gap of 1 m in the succession strata are again exposed in the river. They are harder and more nodular and calcareous than anything seen so far in this section and contain a markedly different fauna, with no typical Lower Bringewoodian forms, dominated by I. orbicularis and A. reticularis. These beds are of an Aymestry Limestone lithology of the Upper Bringewoodian and it is pertinent to note that K. knightii occurs for the first time in these beds. The lowest 1.8 m were collected (samples 016 to 018). The junction between Lower and Upper Bringewoodian is therefore placed in the gap between samples 015 and 016. The boundary is not placed at the bottom of the beds in which bryozoa are abundant since the bryozoa become common gradually and therefore the so-called 'bryozoan bed' has no sharp well defined base but mainly because on faunal and lithological grounds the 'bryozoan bed' resembles the Lower Bringewood Beds most.

The total thickness of beds between the Lower Bringewoodian-Upper Bringewoodian boundary and the lowest Lower Bringewood Beds seen in this section is 37.99 m. Shergold (1967) estimated that in this section the total thickness of the Lower Bringewood Beds is 70.10 m (230 feet) and therefore only beds occurring in the top half of the Lower Bringewoodian were examined.

iv) Ludlow

The Ludlow area was remapped by Holland, Lawson & Walmsley in 1963. It is in this area that the standard sections for the Upper Eltonian - Lower Bringewoodian and Lower Bringewoodian - Upper Bringewoodian junctions were established. However, when visited they were found to be of limited use, since neither exposed the large thickness of Lower Bringewood Beds required for this study. Recently, however, a network of roads has been built through Mortimer Forest by the Forestry Commission. The sections besides these roads were described by Lawson (1973b) and White & Lawson (1978). Two of these sections were found

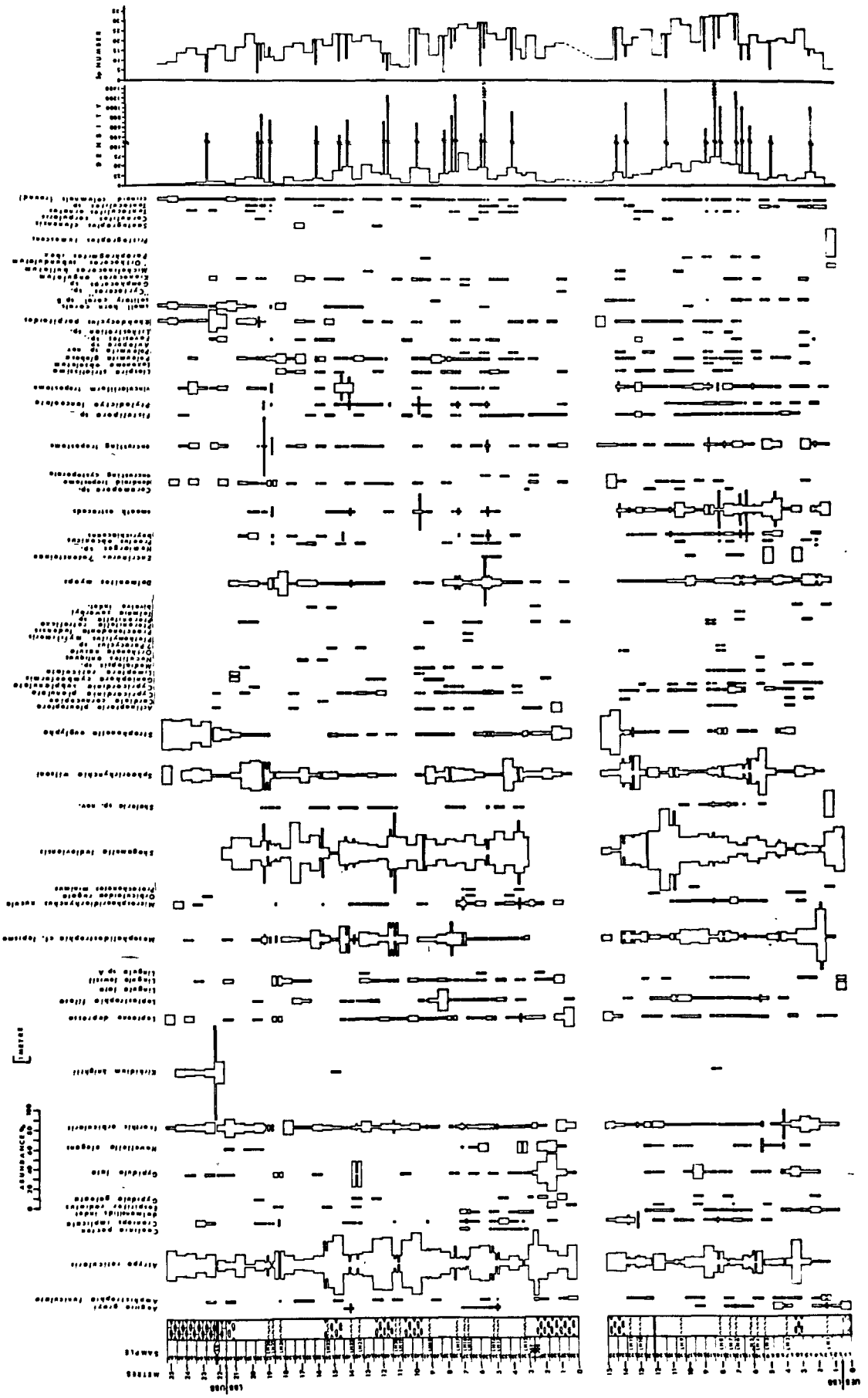


Fig. 3.5 The Lower Bringewoodian succession and fauna at Ludlow

to expose a large thickness of Lower Bringewood Beds, as well as the upper and lower boundaries of the Lower Bringewoodian and they were therefore studied in detail by this author. The results of this present investigation are presented in Fig. 3.5 and discussed below.

At locality 31 of Lawson (1973b) 15.0 m of continuous roadside section, between SO 484727 and SO 486727, were examined and samples L1 to L25 and LH1 to LH11 were collected. The bottom 1.0 m of section was dug out of an overgrown bank by the author (using a spade and trenching tool) to expose the Upper Elton Beds - Lower Bringewood Beds junction. The lowest 0.60 m of section (sample L1) shows well developed flaggy bedding approximately 1 cm thick and yields a low density and diversity fauna dominated by P. tumescens and S. ludloviensis; therefore on both lithological and faunal grounds these lowest beds were assigned to the Upper Eltonian. The boundary is placed at the base of the next sample (L2) since it shows the more calcareous and more irregularly and thickly (4 to 6 cm) bedded strata, with occasional calcareous nodules, so typical of the Lower Bringewoodian. The fauna of these higher beds is also typically Lower Bringewoodian with the incoming of Shaleria sp. nov. (abundant in L2), M. cf. lepisma, L. depressa, A. funiculata, S. euglypha etc. and an increase in faunal density and diversity. The highest beds of this section (samples L24 and L25) are not Upper Bringewoodian as was tentatively suggested by Lawson (1973b, Fig. 1) but are a more calcareous and nodular lithology of the Lower Bringewood Beds containing a fauna showing some Upper Bringewoodian aspects (presumably because of a more Upper Bringewoodian-like lithology).

From a continuous roadside section examined between SO 484714 and SO 486712 (localities 54, 58 and 59 of Lawson (1973b) and section B of White & Lawson (1978)) which includes the Lower-Upper Bringewood Bed boundary, samples L26 to L67, LH12 to LH26 and LK were collected. The lowest 21.6 m of strata exposed in the section belongs to the Lower Bringewoodian. They consist of irregularly and thickly bedded calcareous siltstones with sporadic calcareous nodules; occasionally more nodular and calcareous beds are found. All these beds yield various combinations of typical Lower Bringewoodian fossils such as A. reticularis, A. funiculata, G. lata, L. depressa, M. cf. lepisma, S. ludloviensis, Shaleria sp. nov., S. euglypha etc. The Lower Bringewood Bed-Upper Bringewood Bed junction is placed at the base of sample L62 since the strata above are of hard silty limestone with abundant nodules (typical Aymestry Limestone lithology). This is identical to the position for this junction taken by White & Lawson (1978, p.8). The fauna is also markedly different

above this level as characteristic species of the Lower Bringewood Beds such as L. filosa, S. ludloviensis and Shaleria sp. nov. are absent, or extremely rare, e.g. M. cf. lepisma; instead a typical Upper Bringewoodian fauna dominated by A. reticularis and S. euglypha with corals, bryozoans, S. wilsoni, I. orbicularis etc. and occasional Kirkidium bands is present. Faunal density and diversity in the Upper Bringewoodian are lower than in the Lower Bringewoodian. From the Upper Bringewood Beds 3.6 m of strata above the based junction were examined, samples L62 to L67 and a Kirkidium band at LK were collected.

The Lower Bringewood Beds at Ludlow are dominantly of the thickly (4 to 6 cm) and irregularly bedded calcareous siltstone lithology, on the whole these beds yield abundant S. ludloviensis although M. cf. lepisma, Shaleria sp. nov. or S. wilsoni may rarely become the dominant form for the duration of a small thickness. However, some of the beds are more calcareous and nodular, this lithology often yields A. reticularis as the dominant species, although G. lata or S. euglypha may also be the commonest form. This suggests that these differences in lithology may represent different environments to which differing species were better adapted.

In both Lower Bringewoodian lithologies, thin shell seams, only a few shells thick occur, in which fossils are concentrated in very high densities, 26 of these were found altogether (samples LH1 to LH26). They are identical in appearance to shell seams found at Aymestrey and Leintwardine, although they differ in faunal composition.

An 8 cm thick band of pale grey clay between samples L20 and L21, which is completely unfossiliferous, is interpreted as a bentonite.

The section in the lower Lower Bringewood Beds exposes the lowest 14.4 m of this division while the section in the higher Lower Bringewood Beds exposes the top 21.6 m. As the Lower Bringewood Beds are estimated to be 60.96 m (200 feet) thick in this area (Holland et al. 1963, p.99) it follows that the middle 24.96 m were not observed.

v) Millichope

The area around Millichope was examined by Shergold (1967) and Shergold & Shirley (1968) as part of their investigation of the Wenlock Edge area.

The Upper Eltonian and lower Lower Bringewood Beds are only poorly exposed in minor outcrops in this area. However, a large section through the Lower Bringewood Beds of this area occurs in a quarry at SO 52718911 opposite the northern lodge of Millichope Estate where

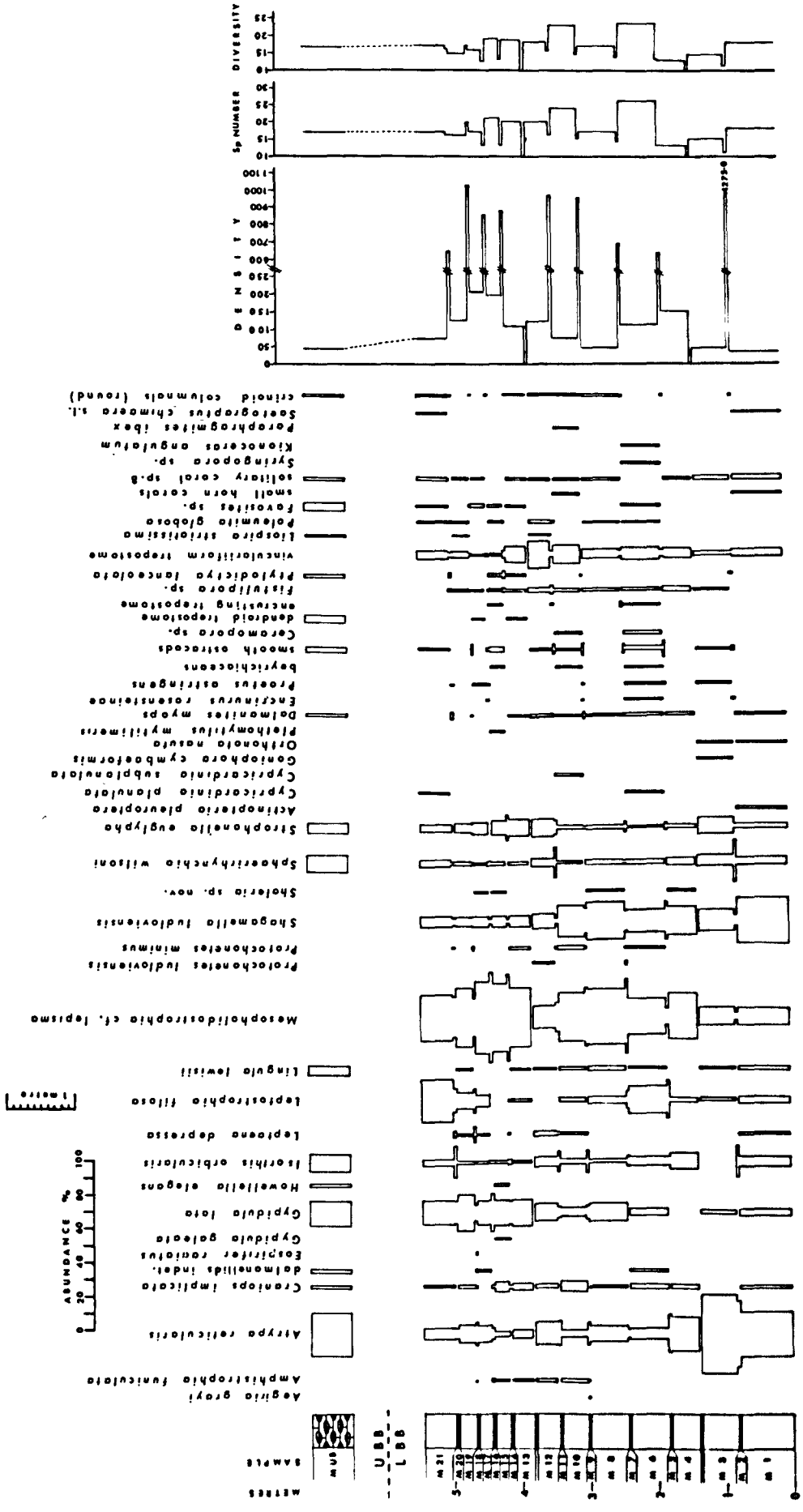


Fig. 3.6 The Lower Bringewoodian succession and fauna at Millichope

5.45 m of beds were examined during the present investigation and samples M1 to M21 were collected (Fig. 3.6). The characteristic Lower Bringewood Bed lithology of calcareous siltstones showing irregular bedding some 4 to 6 cm thick with sporadic calcareous nodules is seen throughout this quarry. The fauna is typically lower Bringewoodian too, A. reticularis, M. cf. lepisma and S. ludloviensis are all common, L. filosa and G. lata are occasionally common and A. funiculata, Shaleria sp. nov., S. euglypha etc. also occur.

Coquinas (samples M2, M5 etc.) with high densities of fossils, compared to the surrounding sediment are quite common. They are lens shaped bodies about 4 cm thick on average and generally about 5 m long, although some are larger than this and may be observed over 15 m in length without both ends being seen. Pale grey clay bentonites occur between samples M3 and M4 and samples M12 and M13, they are both 4 cm thick.

From an examination of Shergold's (1967, Fig. 27) map of this area the beds outcropping in the quarry must form part of the uppermost quarter of the Lower Bringewood Beds, which were estimated at 54.86 m (180 feet) thick by Shergold (1967).

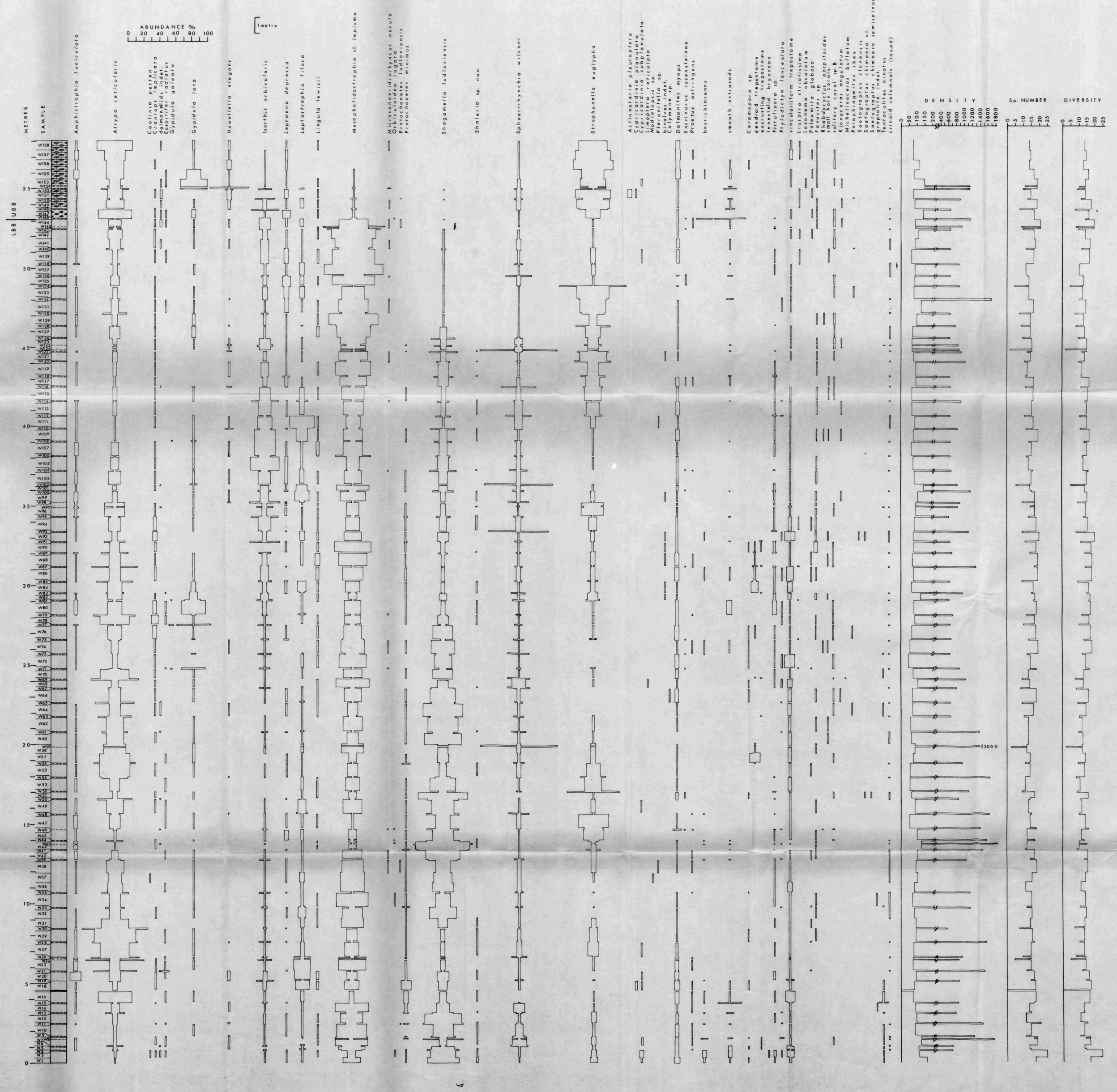
Upper Bringewood Beds were examined in a deep stream channel running parallel to and on the north side of a road at SO 532892. A collection (MUB) was made in hard silty limestones which contained a fauna lacking typical Lower Bringewoodian forms such as S. ludloviensis, M. cf. lepisma, Shaleria sp. nov. etc., but consisting of A. reticularis, G. lata, I. orbicularis, S. wilsoni etc. Faunal density and diversity are somewhat lower in the Upper Bringewoodian than the Lower Bringewoodian.

vi) Woodbury

Woodbury Quarry at SO 743636 is a large quarry in the Abberley Hills which exposes almost the entire Ludlow Series; the beds are slightly overturned here. Phipps & Reeve (1967) mapped the Abberley area as part of their investigation of the Ledbury, Malvern and Abberley Hills. Results of the work carried out by the present author are shown in Fig. 3.7.

The lowest 53.10 m of strata exposed in the quarry are calcareous siltstones with irregular bedding and occasional calcareous nodules; coquinas on average about 4 cm thick and about 5 m long (e.g. samples W4, W6, W9 etc.) occur throughout these beds. These strata yield a Lower Bringewoodian fauna in which S. ludloviensis, M. cf. lepisma

Fig 3·7 THE LOWER BRINGEWOODIAN SUCCESSION AT WOODBURY QUARRY



and A. reticularis are abundant throughout, S. euglypha, I. orbicularis, L. filosa and S. wilsoni are common, and Shaleria sp. nov. also occurs. Therefore on faunal and lithological criteria the lowest 53.10 m of strata in the quarry (samples W1 to S145) can be assigned to the Lower Bringewood Beds. A 5 cm thick, unfossiliferous, greenish grey clay bed, interpreted as a bentonite occurs between samples W16 and W18.

Although when the author visited the quarry (in early 1977) there was 53.10 m of Lower Bringewoodian visible, in a continuous section from their junction with the Upper Bringewoodian to the lowest beds exposed, the amount of these beds seen at any one time varies depending on quarrying operations. As far as can be ascertained their junction with the Upper Eltonian has never been exposed.

The base of the Upper Bringewood Beds is taken at the bottom of sample W146. Above this level the beds are harder, and calcareous nodules become common, occurring both randomly throughout the sediment and in courses, above sample W148 the lithology is of a silty limestone with common calcareous nodules. The increase in hardness of the beds is seen in a steepening of slope in the quarry profile. A marked faunal change occurs with the lithological change at the base of sample W146. The beds now yield abundant A. reticularis and S. euglypha; M. cf. lepisma so abundant in the underlying Lower Bringewoodian strata has rapidly declined to become a very rare form. S. ludloviensis and L. filosa are also extremely rare in the strata in and above sample W146. A suggestion that this boundary was being approached was the rarity of S. ludloviensis above sample W127, although it had been declining in abundance since sample W76, below which it is very common, and the disappearance of Shaleria sp. nov. above W122, as this species is unknown above the Lower Bringewood Beds. The Lower Bringewoodian - Upper Bringewoodian junction is therefore clearly defined on both lithological and faunal changes at the base of sample W146; 5.95 m below the base of a thick (10 cm) pale greenish grey clay bentonite.

However, Watkins (1975, 1979) places the Lower-Upper Bringewood Bed boundary 18.63 m above this bentonite (which he regarded as a fault!). This is strange because he recognised a faunal change (although not a lithological one) 4.87 m below the same bentonite (i.e. only 1.08 m above where this author places the junction). Yet despite the fact that he indicated (Watkins 1975, Fig. 4.2; 1979, Fig. 17) such typical lower Bringewoodian forms as M. cf. lepisma (his M. laevigata), Shaleria sp. nov.

(his S. ornatella) and L. filosa becoming rare above this level (after being so common in the strata below) he regarded this as a 'community' change occurring within the Lower Bringewood Beds, completely ignoring the obvious lithological change which occurs here. What is even more puzzling is that his new 'community' the lower S. wilsoni Association, is shown at Woodbury (Watkins 1975, Fig. 4.2; 1979, Fig. 17) to consist of the following common taxa, S. wilsoni, A. reticularis, M. nucula, I. orbicularis, H. elegans and bryozans, with an absence of any characteristic Lower Bringewoodian forms, this is clearly an Upper Bringewoodian fauna!

The lowest 4.95 m of the Upper Bringewoodian as recognised here were examined and samples W146 to W158 collected.

vii) Perton Lane

The mapping of the area around Perton was carried out as part of an investigation of the northern part of the Woolhope inlier by Tucker (1958). Accounts of the Perton Lane section examined during this study are also given in Squirrell & Tucker (1960) and Curtis et al. (1967). It is in Perton Lane that the Lower Bringewood Beds (the Lower Sleaves Oak Beds of Squirrell & Tucker (1960) and the Lower Tower Hill Beds of Tucker (1958)) of this area are most completely exposed (Tucker 1958, p.226). The results of the present study are given in Fig. 3.8.

The Upper Elton Beds (the Upper Wooton Beds of Tucker (1958) and Squirrell & Tucker (1960)) were examined on the east side of the lane between Tower Hill and Wooton at SO 59253948, where a collection (PUE) was made. These rocks are regularly bedded, approximately 1 to 2 cm thick, flaggy siltstones yielding a low density, low diversity fauna dominated by S. ludloviensis with P. tumescens and little else.

The junction between the Upper Eltonian and Lower Bringewoodian is not exposed, and strata exposed in both sides of the lane, which runs north-east from Copgrove Farmhouse at SO 59643961, were the lowest Lower Bringewood Beds seen, and from an examination of Tucker's map (1958, Fig. 14) must lie within the lowest third of this division. From the 2.82 m of strata exposed here samples P1 to P9 were collected. The lithology here is of irregularly bedded, 4 to 8 cm thick, calcareous siltstones with occasional calcareous nodules; they yield a fauna of common A. reticularis, I. orbicularis, M. cf. lepisma, S. ludloviensis and S. euglypha and are obviously Lower Bringewood Beds. Coquinas, about 5 m long and averaging about 5 cm thick, with high faunal densities,

occur commonly throughout the Lower Bringewood Beds at Perton, just as they do at Millichope and Woodbury.

A large gap in exposure is present before the Lower Bringewood Beds are again exposed in the lane side, where the highest beds are seen. A total of 5.92 m of strata (including a gap of 0.5 m) of the highest Lower Bringewood Beds are exposed on the east side of Perton Lane from SO 59593981 where exposure begins, to the Lower-Upper Bringewood Bed boundary at SO 59583985 and samples P10 to P23 were collected. Apart from the top 1.2 m (samples P22 and P23) these highest Lower Bringewood Beds are very similar in lithology and fauna to those seen in the lower parts of the division back along the lane. The top 1.2 m of Lower Bringewood Beds are extremely nodular and more calcareous; in these beds faunal density drops sharply from values in the lithologies below, and S. ludloviensis and M. cf. lepisma decline in abundance.

The junction between Lower and Upper Bringewood Beds is taken at the base of sample P24, above this the lithology has changed to a hard silty limestone with abundant calcareous nodules and yields a completely different fauna from that of the Lower Bringewoodian beneath. M. cf. lepisma is absent now and S. ludloviensis extremely rare, corals have become more important while A. reticularis and I. orbicularis dominate the assemblage. It is pertinent to note that K. knightii occurs for the first time in these beds. A total of 1.80 m of the Upper Bringewood Beds (Upper Sleaves Oak Beds of Squirrell & Tucker (1960) and Upper Tower Hill Beds of Tucker (1958)) were examined and samples P24 to P26 were collected.

The boundary between Lower and Upper Bringewood Beds is therefore placed at the same position in the succession as Tucker (1958), Squirrell & Tucker (1960) and Curtis et al. (1967) considered it to be and is clearly definable on both lithological and faunal criteria. Watkins (1975, 1979), however, considered that the remaining 9.0 m of strata exposed above the boundary as defined here, as well as the 5.92 m below it, in this outcrop, were all Lower Bringewoodian since they were all supposed to contain a 'community', the lower S. wilsoni Association, which he considered to indicate this unit. This is clearly not so, since the Lower-Upper Bringewoodian junction occurs in the middle of this outcrop and is defined by well marked lithological and faunal changes as discussed above. Watkins (1975, 1979) erroneously claims that these changes do not exist.

The total thickness of the Lower Bringewood Beds in Perton Lane

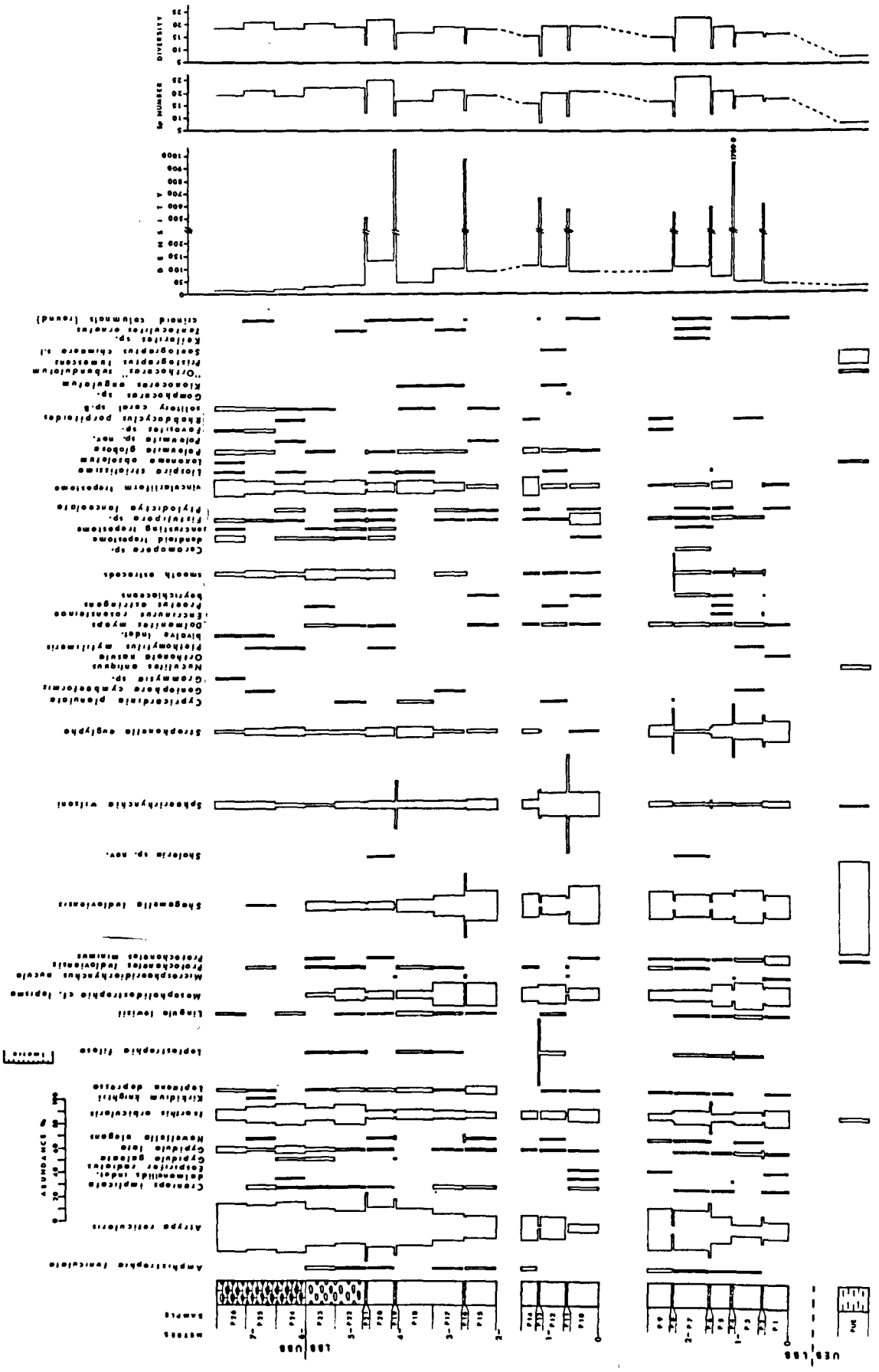


Fig. 3.8 The Lower Bringewoodian succession and fauna at Perton Lane

has been estimated at 76.20 m (250 feet) by Tucker (1958) and as only 8.74 m were found to be outcropping the majority of the division, in this area, is unexposed.

viii) Usk

The area around Usk was mapped by Walmsley (1955, 1959); good localities are also given in Curtis et al. (1967).

At Porth-llong the Lower Bringewood Beds (the Upper Forest Beds of Walmsley (1955, 1959)) are exposed in a small quarry (considered by Walmsley (1955) to be the best exposure of these beds) by the roadside at ST 35189777. Here 3.22 m of beds were examined by this author (see Fig. 3.9) and samples U1 to U11 collected from irregularly bedded (3 to 6 cm thick) calcareous siltstones with sporadic calcareous nodules; highly fossiliferous coquinas (e.g. samples U2, U4 etc.) identical to those at Perton, Woodbury and Millichope also occur. These beds yield a fauna with common A. reticularis, I. orbicularis, M. cf. lepisma, S. ludloviensis and S. wilsoni which definitely indicates the Lower Bringewood Beds.

If the road is followed to the north, from the old quarry, for just over 100 m then strata are again exposed. They are fairly regularly bedded, flaggy (1 cm thick) siltstones which yield a low density and low diversity fauna dominated by S. ludloviensis; a few indeterminate graptolites are present. Elements of the fauna which are so common or typical of the Lower Bringewoodian are absent or rare in these beds. These are the Upper Elton Beds (the Lower Forest Beds of Walmsley (1955, 1959)), a sample (UUE) was collected from near the top of the exposure.

The thickness of strata unexposed between the above two localities is estimated at 10 m and the boundary between Upper Eltonian and Lower Bringewoodian must lie within this gap, so that the beds in the quarry must be low in the Lower Bringewood Beds.

Strata judged to be slightly higher in the Lower Bringewood Beds, from Walmsley's (1959) map, were examined at the side of a track at ST 32769853 near the eastern end of Llandegfedd Reservoir dam. Here 3.29 m of strata were examined and samples U12 to U22 collected. The beds are identical in lithology to those seen in the quarry mentioned above but they yield a slightly different fauna e.g. A. reticularis is commoner and S. wilsoni is rarer, on the whole the two faunas are very similar, however.

The Upper Bringewood Beds (the Lower Llanbadoc Beds of Walmsley (1955, 1959)) were examined in the large old quarry at SO 375002. They

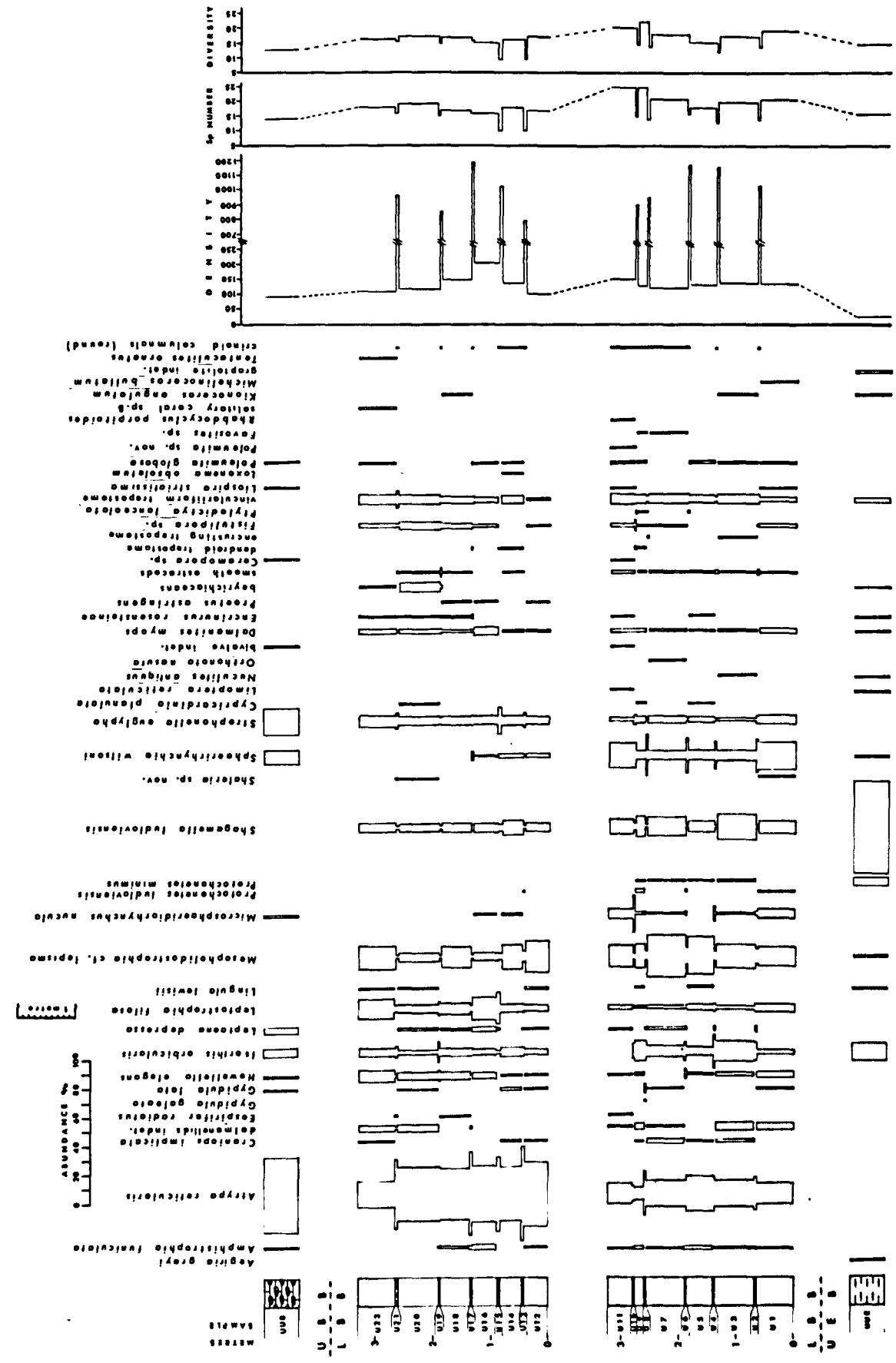


Fig. 3.9 The Lower Bringewoodian succession and fauna at Usk

are hard, nodular, silty limestones with a fauna in which A. reticularis is abundant and S. euglypha and S. wilsoni are common. Forms common in the Lower Bringewoodian such as M. cf. lepisma, S. ludloviensis and L. filosa etc. are absent. A sample (UUB) was collected.

The thickness of combined Lower and Upper Bringewoodian is given by Walmsley (1959), as he did not map out the junction between them, as 70.10 m (230 feet). Assuming the Lower Bringewoodian are half this thickness then they are 35.05 m thick, of which a total of 6.61 m were examined.

ix) Brookend borehole

The Brookend borehole gives the most south-easterly information about the Lower Bringewood Beds. It was examined at I.G.S. (London) by kind permission of Dr. D. White. The borehole was drilled at SO 68770230 near Vine Farm, Brookend. The borehole passed through the Downtonian, and Ludlovian as far as low Eltonian (Cave & White, 1978). Results of this author's examination of the core are discussed below and presented in Fig. 3.10.

The Upper Eltonian and Lower Bringewoodian lithologies seen in the borehole are similar; both are of calcareous siltstones with sporadic calcareous nodules and at first the Upper Elton Beds-Lower Bringewood Beds boundary is not obvious. However, White (pers. comm. 1978) takes the boundary at 228.60 m (750 feet) depth, since coquinas, so characteristic of Lower Bringewoodian strata this far east are rare below this level and were not found below 232.26 m (762 feet) depth (i.e. ES81 is the lowest) he took this as a lithological change possibly indicating the boundary (cf. Shergold & Shirley 1968, p.124). The strata below 228.60 m also appear to be less silty, more muddy and contains very little shell debris compared to overlying beds. There is also a fall in faunal density and diversity below 228.60 m depth, which is always seen when passing from the Lower Bringewoodian to Upper Eltonian. Although the fauna above and below this boundary appears similar, it is more restricted below the boundary and L. filosa, M. nucula, L. depressa, A. reticularis, M. cf. lepisma, H. elegans and A. funiculata are all rare or absent which strongly suggests that these beds are Upper Eltonian, although S. euglypha is unusually common, while S. ludloviensis is somewhat rarer than may be expected from examining other sections in the Upper Elton Beds. Therefore on faunal and lithological criteria the junction can be placed at 228.60 m depth i.e. at the base of sample E39. Dr. Dorning confirms this from an examination of

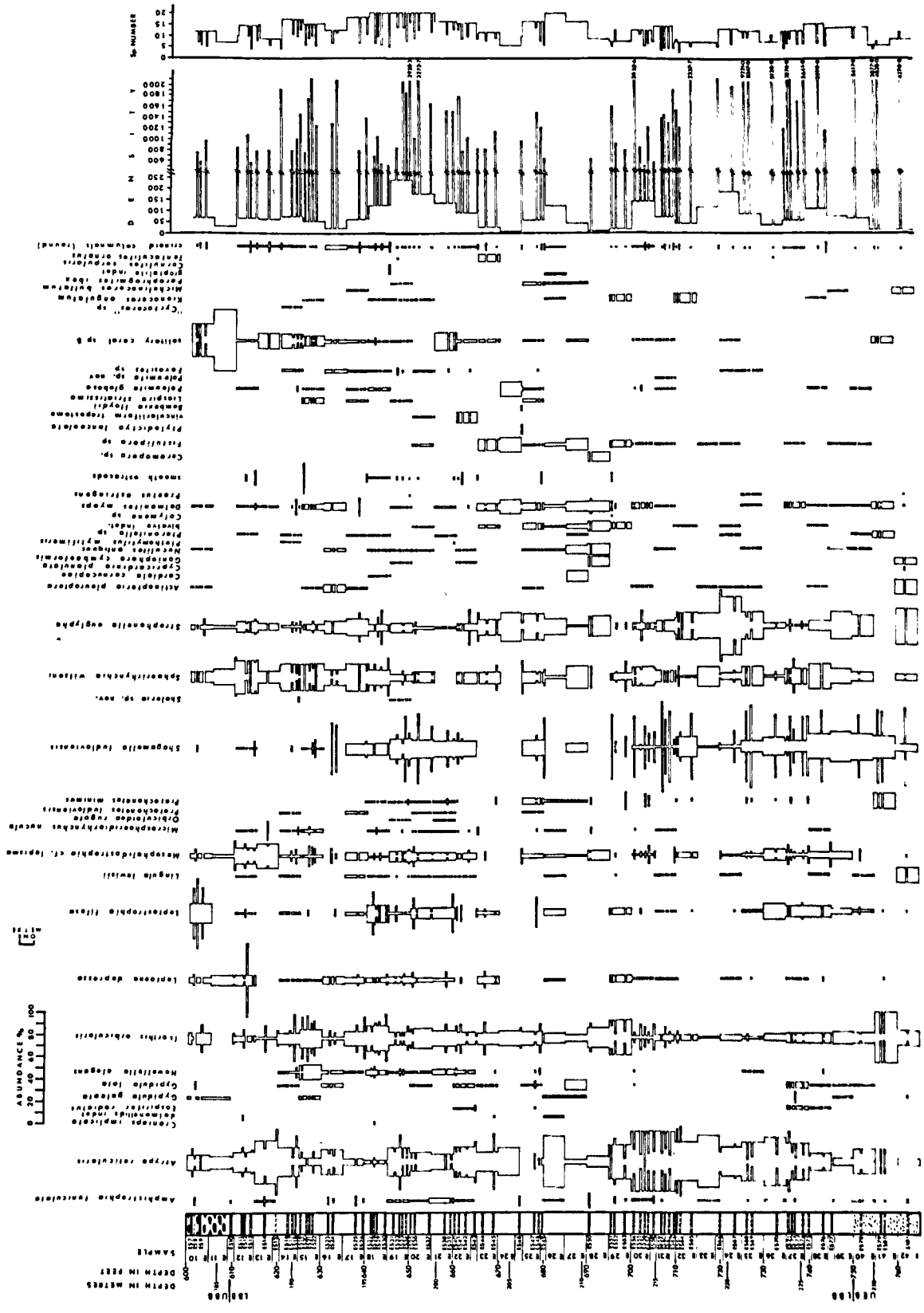


Fig. 3.10 The Lower Bringewoodian succession and fauna in the Brookend borehole

palynological assemblages from which he suggests the boundary must lie between 220.47 m (723 feet 4 inches) and 230.48 m (756 feet 2 inches) depth (Dorning pers. comm. 1978).

The Lower Bringewoodian-Upper Bringewoodian junction is considered to be at the base of sample E11 i.e. at 185.87 m (609 feet 10 inches) depth where a lithological change to a more nodular and calcareous lithology occurs. A faunal change is also obvious at this level where solitary coral sp. B becomes abundant. Dorning (pers. comm. 1978) from palynological evidence considers the boundary to lie between 191.00 m (626 feet 8 inches) and 175.56 m (576 feet) which seems to confirm this.

The Lower Bringewood Beds therefore occur in the borehole between 185.87 m and 228.60 m depth and are thus 42.73 m thick.

SEDIMENTOLOGY

In order to successfully interpret the distribution pattern and abundance of fossil organisms in the Lower Bringewood Beds it is obviously necessary to know in what environment these organisms lived. The sedimentology of the shelf Lower Bringewoodian is therefore considered and environmental interpretations made on this evidence. Detailed petrographic work was not undertaken but about 10 to 20 thin sections and over 100 polished sawn cut blocks of each lithology were examined. The sedimentology of the Upper Elton Beds and Upper Bringewood Beds are considered briefly so that the Lower Bringewood Beds may be considered in context.

Bentonites

These were found in all divisions of the Ludlow examined during this study. They are thin beds (those seen were between 4 and 10 cm thick) of pale creamish grey (when weathered) or soapy green (when fresh) coloured, very plastic clay, peppered with visible, euhedral biotite flakes. They are internally homogeneous, unfossiliferous and show no signs of bioturbation. The lower contacts of these clays are always sharp and the upper contacts usually sharp, although sometimes the tops grade rapidly through a biotite rich layer into the overlying sediment. In all cases they were seen to be continuous across available outcrop, but R. Marsh (1976) records examples of bentonites lensing out across sections, suggesting they were concentrated into seafloor lows by currents and concluded that their use in correlation was minimal. They provide evidence of volcanic episodes during the Upper Eltonian and Bringewoodian.

Upper Elton Beds - Facies 1 - The Flaggy Siltstone Facies

This is the dominant facies of these beds, occupying their entire thickness in the sections at Aymestrey, Leintwardine, Ludlow, Wenlock Edge, Perton, Usk and the Malvern Hills; data for the following description was collected both from this author's observations and an examination of the published literature on each of the shelf areas that have been mapped (p.2).

The beds of this facies are olive grey, well developed flaggy siltstones with the flags generally about 1 cm thick, it is easy to break off large sheets of rock from exposures of this lithology. Mottling of these sediments and trace fossils are rare throughout most of this facies, although, they appear to become commoner at Usk where, significantly, the flaggy bedding is less well developed. These beds may show laminations with darker more argillaceous laminae up to 3 mm thick. Shell debris is virtually absent, most brachopod shells are still articulated and all shells show preservation of fine features (e.g. the spines of S. ludloviensis) suggesting they have been undisturbed by currents strong enough to cause significant transportation. Coquinas are extremely rare (only one was found). In this lithology rare ellipsoidal calcareous nodules occur, they have long axes which are up to 10 cm long and are composed almost entirely of micrite and little else except rare quartz and mica grains. Occasionally interbedded with these strata are highly calcareous siltstones which are usually a few centimetres thick.

Near to the shelf edge (i.e. at Leintwardine, Aymestrey and Ludlow) these beds commonly show the development of crinkle marks and occasional slumps occur, such sedimentary structures indicate that this sediment moved towards the basin (Williams & Prentice 1958; Lawson 1973a).

In thin section the flaggy siltstones are seen to consist of many silt sized subangular to subrounded quartz grains and much clay sized material, with rare micas and plagioclase in a matrix of micrite. Many of the micas and other platy minerals show a sub parallel orientation to bedding. Compared to the bioturbated siltstone facies quartz appears to be finer and clay material more abundant in these beds.

Interpretation. The fine grain size, presence of substantial clay material and lack of shell debris suggests that these deposits accumulated in a low energy very distal shelf environment, in this quiet environment fine grained material settled out of suspension. The lack of storm deposits indicates that these sediments accumulated beyond the reach of

such activity. The occurrence of crinkle marks and slumps in the sediments of the shelf edge indicate an instability at the shelf margin and a basin influence which is further suggested by the rarity of bioturbation, which probably indicates inadequately oxygenated conditions due to infrequent mixing of the water in this quiet water environment (Dapples 1942; Rhoads & Morse 1971; Shafer 1972; Rhoads 1975). This is not to suggest that the environment was anoxic, since bioturbation is present, however, these offshore deposits are thought to have lain beyond the zone of mixed and fully aerated surface waters. Bioturbation increases somewhat away from the shelf edge and the more extensive bioturbation seen at Usk probably reflects a more oxygenated bottom due to increased mixing of the water from greater turbulence.

Upper Elton Beds - Facies 2 - The Brookend Facies

This facies is only found in the Upper Elton Beds of the Brookend borehole. It is similar to that of the bioturbated siltstone facies of the Lower Bringewoodian, which is described below, in that the strata are intensely bioturbated and have an extremely mottled appearance in polished section and also lack flaggy bedding. However, in all other features it is identical to the flaggy siltstone facies.

Interpretation. The increase in bioturbation away from the shelf edge in the Upper Elton Beds reaches its maximum in this facies suggesting fully oxygenated bottom conditions, allowing full reworking of the sediment by benthic organisms, probably as a result of increased turbulence mixing the water more completely. The rarity of coquinas and storm produced sedimentary structures indicates that this area was still beyond the range of storm sedimentation for most of the Upper Elton and it is thought that turbulence was still less than in the overlying Lower Bringewood Beds.

Lower Bringewood Beds - Facies 1 - The Bioturbated Siltstone Facies

This is the dominant facies of the Lower Bringewood Beds, occupying the complete thickness of this division at Aymestrey, Millichope, Woodbury, Usk and in the Brookend borehole; it is also the dominant lithology in the remaining shelf sections visited at Perton, the River Onny, Ludlow and Leintwardine.

This facies consists of calcareous siltstones with occasionally interbedded coquinas. These two lithologies will be considered in turn.

a) The olive green, calcareous siltstones are irregularly bedded, with units generally 3 to 8 cm thick that may die out or thicken when followed

laterally. In fresh exposures (e.g. Woodbury Quarry), however, this irregular bedding is absent and the beds are largely massive with only interbedded coquinas defining the bedding. At Woodbury it is possible to trace such massive bedding in the fresh faces to older weathered faces showing the irregular bedding. This irregular bedding is therefore thought to be a weathering feature. Watkins (1975, 1979) made similar observations.

In thin section these siltstones are seen to be poorly sorted and matrix supported, consisting mostly of equidimensional rather angular to quite rounded silt grade quartz, with rarer, randomly orientated micas, feldspars, bioclasts and clay minerals set in a micrite matrix. Quartz is always more abundant then clay, although there appears to be a gradation across the shelf from Aymestrey to Brookend with sediments nearer the shelf edge having more clay and less quartz. Macroscopic shell fragments may also be present and are far commoner in sections away from the shelf edge. The average number of macroscopic shell fragments per cm^2 in the polished faces of 15 samples, of similar size, from each locality varies from 0 at Aymestrey and Leintwardine to about 1 at Ludlow and rises to greater than 4 in sections at Woodbury, Usk etc. in the shelf inliers.

In polished section complex mottling is seen with darker, clay rich and lighter siltier areas (Plate 1, Fig. 1). A few discrete traces are occasionally discernable, these may be either rare horizontal, slightly sinuous, burrow up to 3 mm in diameter and up to 10 cm long or subvertical burrows up to 6 mm in diameter which may be filled with shell debris; Chondrites is also quite common. Few sedimentary structures are visible in these sediments, only in the shelf inliers, especially at Usk and in the Brookend borehole where the mottling is not quite so intense are the remnants of parallel laminated silt and mud or graded beds from fine sand to silt seen; these often overly shell beds which are interpreted later as storm deposits.

In these sediments calcareous nodules occasionally occur, they are ellipsoidal in shape and mostly have their longest axes (always parallel to bedding) between 4 and 15 cm long. These nodules may occur randomly scattered throughout the sediment or in courses. Only rarely do they have shell material contained within them, but when they do it is preserved uncrushed, whereas in the siltstones around the nodule, fossils usually show signs of compaction. The surrounding siltstone arches over and under the nodules. These observations confirm the views

EXPLANATION OF PLATE 1

Sediments Of The Bioturbated Siltstone Facies

Fig. 1 Typical appearance of the bioturbated siltstone facies showing mottling produced by intensive bioturbation of the sediment (x 1). Lower Bringewood Beds, Woodbury Quarry. Sample W66.

Fig. 2 Fairly thick layer of bioclasts grading upwards into bioturbated siltstone (x 1). Typical example of a group 1 shell bed, interpreted as a quite proximal storm bed, cf. Figs. 6 and 7 below. Lower Bringewood Beds, Woodbury Quarry. Sample W95.

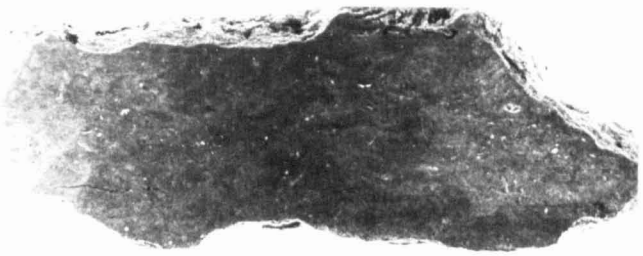
Fig. 3 Laminated siltstone unit overlying bioclastic bed, group 1 shell bed (x 1.1/4). Lower Bringewood Beds, Usk. Sample U10.

Fig. 4 Sharp erosive base of a bioclastic unit of a typical group 1 shell bed (x 3½). Lower Bringewood Beds, Woodbury Quarry. Sample W71.

Fig. 5 Group 1 shell bed in bioturbated siltstone (x 3/4). Note sharp base and burrowed upper surface of bioclastic bed. Burrow (?) in centre. Lower Bringewood Beds, Brookend borehole. I.G.S. sample CV5055.

Fig. 6 Thin layer of bioclasts in bioturbated siltstone (x 2½). Typical example of a group 2 shell bed, interpreted as a distal storm deposit, cf. Figs. 2 to 5 above. Note upward grading. Lower Bringewood Beds, Ludlow. Sample LH17.

Fig. 7 Appearance of the upper surface of a group 2 shell bed (x 3/4). Lower Bringewood Beds, Ludlow. Sample LH7.



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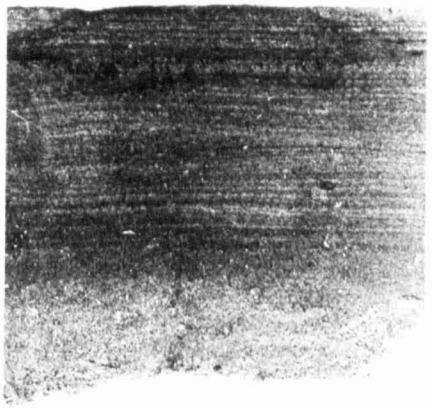

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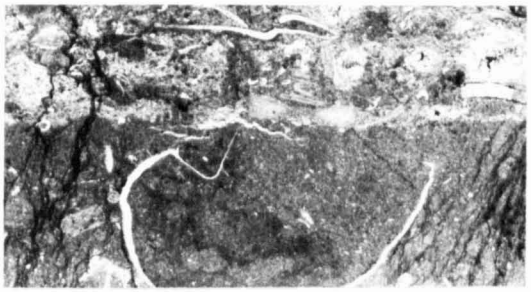

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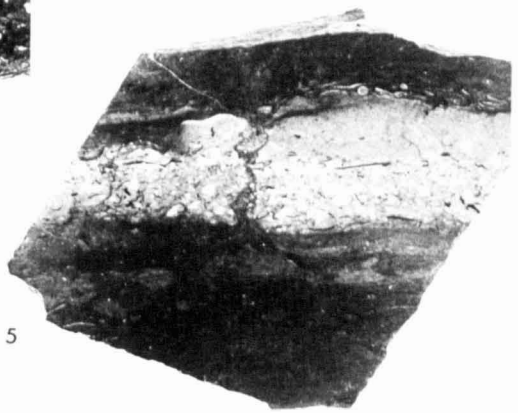

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PLATE 1

of previous authors that the nodules document an early movement of carbonate within the sediment which is post-depositional but pre-compactional. In thin section the nodules are seen to be almost entirely composed of microsparite with rare quartz and mica grains. Any fossils within the nodules have been replaced by a sparry calcite matrix, although the original structure of the shell is defined by dust lines.

Within this lithology shells show no evidence of current transport, many still possess very delicate spines (e.g. S. ludloviensis) or frills (A. reticularis), each species shows a wide range of shell size and nearly equal numbers of opposite values in disarticulated specimens, although, many are still articulated and finally infaunal forms are found in situ; for example out of 266 Lingula lewisii specimens collected from this lithology 81.2% (216) were found in life position. The associations of shells found in this lithology therefore correspond to the disturbed neighbourhood assemblages of Scott (1974) in which shells show no evidence of current transport although they may have moved from their life position due to the activities of burrowers, predators, gravity or weak currents.

Interpretation. The most distinctive aspect of this lithology is the lack of sedimentary structures and the complex mottling they show. Moore & Scrutton (1957) showed that the creation of such mottles is a secondary feature produced by benthic animals living and feeding in the sediments. They conducted experiments in which regular layered sediment was placed in the base of tanks, and showed that these original layers were destroyed when benthic organisms were introduced. As they burrowed into the sediment the initial layers were distorted and sediment was suspended in and about the burrows, finer material was winnowed and coarser material concentrated, until eventually an indistinctly mottled sediment was produced.

The fact that this complex mottling and lack of sedimentary structures is the result of extensive and intensive deformative bioturbation is also suggested by the remnants of laminated and graded bedding which are seen occasionally in areas of slightly less intense mottling.

Such sediments correspond to modern bioturbated shelf sediments, the shelf mud/silt facies of Reineck & Singh (1973). These sediments accumulate by the settling of suspended silt and clay under quiet, low turbulence, conditions, below wave base and away from the shore. Sedimentation is slow enough for the continued activity of burrowers to

prevent the preservation of most of the sedimentary structures formed. Howard (1975) concluded that sediments in which the complete biogenic destruction of the primary fabric and structures had taken place owed their origin more to the time available for biogenic activity per unit accumulation of sediment (through slow and continuous sedimentation) than the density of animals or the frenzy of their activity. Rhoads (1975) also suggested that complete biogenic reworking of the sediment indicates low sedimentation rates, together with a sufficiently well oxygenated environment.

Although these calcareous siltstones are remarkably similar over the whole shelf, the decrease in clay and increase in the proportion of quartz and the amount of shell debris away from the shelf edge, suggests a gradual increase in turbulence in this direction.

b) Coquinas often occur interbedded with the bioturbated silt lithology (and also the nodular bioturbated silt lithology discussed later). They are blue grey, poorly sorted bioclastic limestones consisting of abundant shells and shell debris (mostly bryozoans and brachiopods) together with rare quartz, micas and feldspar grains in a matrix of microsparite; sparite grew in any voids e.g. the interior of shells. Rare mudclast inclusions are also noted. The organic fragments and the matrix adjacent to them often show the development of sparite (the original shell structure, in these cases, being seen as dust lines within the sparite mosaic) and detrital grains such as quartz, mica and feldspar may commonly be seen enclosed by sparite crystals, furthermore it is quite apparent that the greatest concentration of calcite in the bioturbated siltstone facies occurs around these shell beds; these facts suggest that the 'limestone' nature of these shell beds is secondary, with the carbonate probably derived from the shells, and is not a depositional feature. Watkins (1979) came to similar conclusions. As the fossil material in the shell beds is uncrushed, compared to the surrounding siltstones, this carbonate enrichment is post-depositional but pre-compactional.

Many shells within the coquinas are disarticulated and some show signs of breakage, many are convex up but they can occur in any orientation; indeed in most shell beds the shells appear to show no preferred orientation at all and may be observed in all positions. Shells may often be imbricated; imbrication of L. depressa and S. euglypha valves is quite common. The shells are packed together to give high density assemblages with abundant shell debris surrounding them. All shell beds show a marked increase in faunal density compared to the

sediments around them, values of fossil density in shell beds are usually 10 times greater than those in the surrounding sediment. These faunal associations are analagous to the transported assemblages of Scott (1974).

The number of fossil species in shell beds is, however, nearly always less than in the surrounding sediment. This is mainly due to the fact that infaunal remains are extremely rare in shell lenses. Watkins (1975, 1979) has made similar observations. Out of 276 specimens of Lingula lewisii collected from the Lower Bringewood Beds only 10 were found in shell beds and of these 4 were found articulated at 90° to bedding and were therefore assumed to have burrowed into the shell bed after its deposition, thus only 6 specimens were originally deposited at the time of the bed's formation i.e. just over 2% of the total number found. Similarly out of 289 specimens of burrowing bivalves collected from the Lower Bringewoodian less than 1% were found in shell beds. It is therefore concluded that epifaunal remains are significantly concentrated into shell beds relative to infaunal remains, which are almost absent from them.

These coquinas are lenticular in shape and vary in thickness from a few shells to 8 cm and in length from a few metres to greater than 15 m without both ends being observed.

In each section examined the shell beds show different average thickness, frequency of shell beds per metre of section and percent of stratigraphic thickness they make up. All the above features vary across the shelf (Table 3.1, Fig. 3.11) and on these and other criteria it is possible to divide these shell beds into 2 groups.

Group 1 - Those from Millichope, Woodbury, Perton, Usk and the Brookend Borehole. In these sections the shell beds are generally 3 to 5 cm thick and the average thickness in all sections is greater than 3 cm. Also in all these sections shell beds make up between 4.95% and 7.18% of the Lower Bringewood Beds and there is an average thickness of sediment between successive shell beds of less than one metre. All shell beds in this group have sharp, flat erosional bases of low relief (Plate 1, Figs. 4,5) which in several cases truncate subvertical burrows in the underlying sediment (cf. Bowen et al. 1974). These shell beds grade up into the finer overlying sediment (Plate 1, Figs. 2, 5), reverse grading was also rarely seen. The tops of the beds are often strongly bioturbated (Plate 1, Fig. 5). Some shell beds (Plate 1, Fig. 3) may also be seen forming the basal layers of finely laminated

SECTION	TOTAL THICKNESS OF STORM BEDS IN m	NUMBER OF STORM BEDS	AVERAGE THICKNESS OF STORM BEDS IN m	TOTAL THICKNESS OF LOWER BRINGEWOODIAN EXAMINED IN m	STORM BEDS PER m OF SECTION	STORM BED % OF LOWER BRINGEWOODIAN	
AYMESTREY	0.020	4	0.005	21.00	0.19	0.10	GROUP 2 SHELL BEDS
LEINTWARDINE	0.005	1	0.005	30.60	0.03	0.02	
RIVER ONNY	0.015	1	0.015	10.69	0.09	0.14	
LUDLOW	0.160	26	0.006	36.00	0.72	0.44	
MILLICHOPE	0.370	9	0.041	5.45	1.65	6.79	GROUP 1 SHELL BEDS
WOODBURY	2.630	70	0.038	53.10	1.32	4.95	
PERTON	0.460	9	0.051	8.74	1.03	5.26	
USK	0.420	10	0.042	6.61	1.51	6.35	
BROOKEND	3.070	68	0.045	42.73	1.59	7.18	

Table 3.1. Thickness and frequency of storm deposits in the Lower Bringewoodian shelf sediments.

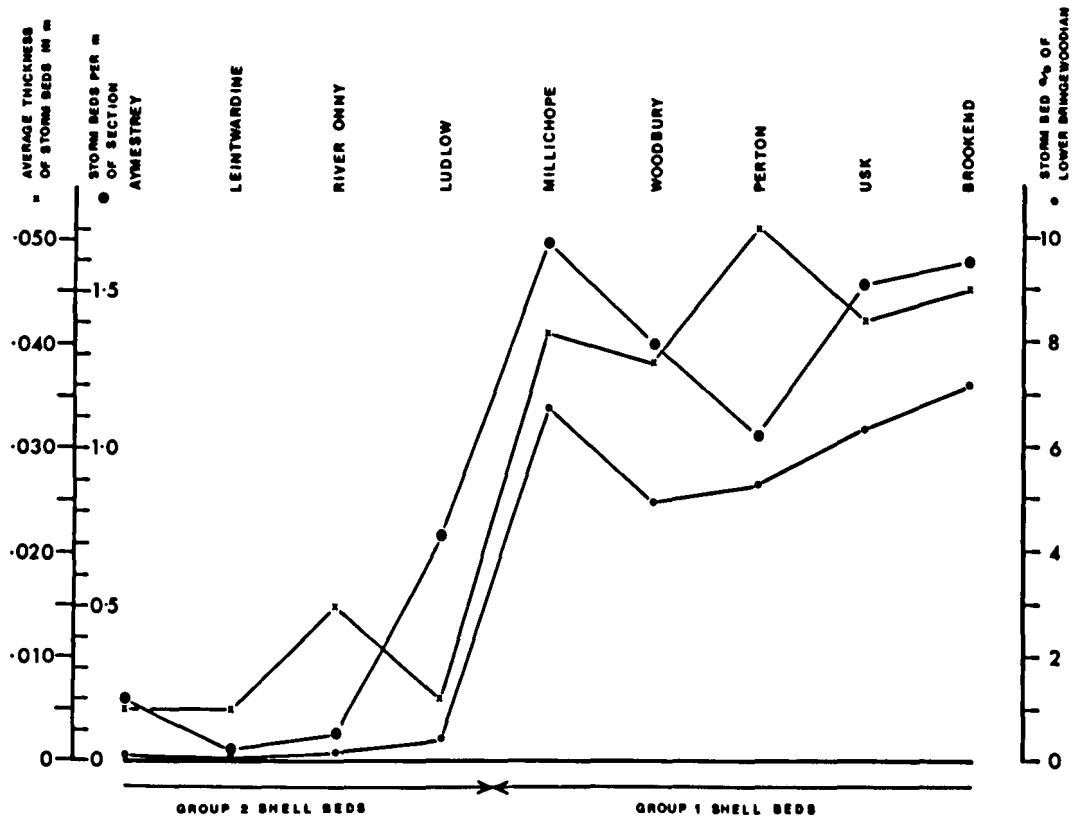

Fig. 3.11. Variation in the frequency and thickness of Lower Bringewoodian storm deposits between shelf sections.

silt sheets (the lighter laminae being richer in silt and the darker laminae containing more mud). In some cases only relicts of this laminated silt sheet are seen amongst extensively bioturbated sediment and in other cases bioturbation extends down to and into the top of the shell beds (Plate 1, Fig. 5, left hand side). These observations suggest that shell beds, identical to those discussed above, but without an overlying graded unit or laminated silt sheet may have been deposited with one or the other overlying unit, but due to subsequent biogenic reworking all evidence of it has been destroyed. Shell fragments and debris are very abundant in these shell beds, some fossils show signs of breakage and many are disarticulated. The fauna of the shell beds is sometimes similar to that of the surrounding sediments but may be markedly different, suggesting sorting or transportation has taken place.

Group 2 - Those shell beds from Aymestrey, Leintwardine, the River Onny and Ludlow (see Fig. 3.11, Table 3.1). In these sections shell beds are always less than 1 cm thick (except for the 1.5 cm thick one in the River Onny section) and have an average thickness between 0.5 and 0.6 cm. In all these sections shell beds make up less than 0.5% of the total Lower Bringewood Bed thickness observed and there is an average thickness of greater than 1 metre between each shell bed. They are therefore thinner, rarer and so make up less stratigraphic volume than those of group 1. Although the bases of these shell beds may be well defined by the sudden increase in bioclasts and calcareous material (Plate 1, Fig. 6) they never appear to be erosional. Bioturbated sediment lies directly below and they quickly grade into such material above, sometimes they are directly overlain by bioturbated sediment and in these cases it is possible that any original grading may have been destroyed by subsequent biogenic reworking. Shell fragments and debris are not as common in shell beds of this group as in group 1 and most of the shells are unbroken, although many are disarticulated (Plate 1, Fig. 7). The shell beds of this group are never overlain by thick graded or laminated silt sheets. The fauna of these shell beds is often very similar to that of the surrounding sediments.

Interpretation of Group 1 shell beds - These coquinas occur interbedded with extensively bioturbated silt. They consist of concentrations of mainly disarticulated and sometimes broken shells with much shell debris and have sharp erosive bases of low relief. The shell bed grades up into the overlying sediment or may be overlain by finely laminated silts. The top is usually strongly bioturbated.

The origin of such deposits is thought to be as follows. During severe storms the top layer of sediment (a bioturbated silt) was eroded by waves and the shells of both living and dead organisms were suspended, together with clouds of silt and pieces of consolidated mud which may have been ripped up, this whole suspension cloud was then swept forward by the storm waves. Erosion of the shelf was not extensive since lingulids and burrowing bivalves were rarely scoured from their burrows. With a decrease in energy, as the storm passed on, the shells settled out onto the sea floor as a coarse basal layer, especially in shallow depressions (giving them a lens shape). The chaotic orientation of the shells results from their rapid settling from suspension (Middleton 1967). After the storm, sand and silt eroded from the coast is transported seaward by retreating waves as suspension clouds. With a decrease in energy sediment settled out of these suspension clouds to give graded or laminated units. Bowen et al. (1974) noted it was possible to have reverse grading above shell beds, as seen rarely in the Lower Bringewoodian, if locally derived resuspended silt settled out before that from the seawards transport of coarser material from storm surges or retreating waves. Post storm conditions are marked by a repopulation of the bottom by benthic organisms, some of which burrow into the newly deposited sediment. In time such burrowing activity may destroy all sedimentary structures above the shell bed.

Shell beds with sedimentary structures identical to those of the Lower Bringewood Beds are known from the Llandovery of the Welsh Borderland (Bridges 1975), the Devonian of New York (Bowen et al. 1974), the Jurassic of Wyoming and Montana (Brenner & Davies 1973), the Wenlock of S.W. Ireland (Watkins 1978b), the Upper Muschelkalk of S.W. Germany (Aigner et al. 1978; Aigner 1977, 1979) and the Ludlovian of the Welsh Borderland (Watkins 1979). All these authors interpret such deposits as the result of storm action in a way similar to that outlined above. Modern sediments showing sedimentary structures identical to those seen in the Lower Bringewoodian coquinas have been described from the Mediterranean (Reineck & Singh 1971) and the North Sea (Gaddow & Reineck 1969; Reineck & Singh 1972); they are formed by storm surges transporting nearshore silt and sand toward the open sea. Gaddow & Reineck (1969) suggested that this sediment could be transported up to 45 km from the coast and in depths of water up to 40 m. It is thought unlikely that shells travelled such large distances, as often the faunal composition of the shell bed bears a stronger resemblance to that of the

sediment surrounding it than the faunal composition in an adjacent section, say 10 km away. Although the shells of these coquinas have obviously been transported (suffering disarticulation together with some breakage and fragmentation in the process) from their area of origin it is possible that in many cases they have been transported only a few kilometres at the most, rather than the tens of kilometres that the silt and sand which overlie them may have moved. The similarity or difference in the faunal composition of the shell beds and that of the surrounding sediment depends on the amount of transport (i.e. winnowing and sorting) that the shells in the storm deposit have undergone.

The greater frequency and stratigraphic volume occupied by these shell beds, compared to those of group 2, together with their associated sedimentary structures suggest that these are more proximal storm deposits than those of group 2. Such conclusions are consistent with the work of Aigner et al. (1978) and Aigner (1979) on the Upper Muschelkalk of S.W. Germany and Brenchley et al. (1979) on the Ordovician of Norway. All these authors note that storm deposits thin and become rarer distally.

Interpretation of group 2 shell beds - These shell beds consist of concentrations of mostly disarticulated shells, although some are still articulated. The shell beds are lens shaped and occur interbedded with bioturbated silt. They never show an erosion surface at their base and are usually only a few shells thick, containing only a little shell debris and far less than those of group 1 shell beds. They grade quickly into the overlying bioturbated sediment or such sediment rests directly on top of them.

Their origin is thought to be due to high amplitude swells passing over the sediment-water interface. Such swells create hydraulic lift of the bottom which results in the suspension of the upper sediment layer together with any living or dead shells on or within it. After the swell has passed the shells settle out of suspension first, with no dominant orientation (Middleton 1967), followed by the resuspended sediment with the coarsest material settling out first to give a graded deposit. Although, this grading may be later destroyed by bioturbation after the benthos has repopulated the sediment. Such swells must only suspend the topmost sediment since burrowing bivalves and lingulids are not eroded out of their burrows.

Swells of sufficient magnitude to affect the shelf sediment must be storm generated since, as we have already established, normal wave

action did not extend down to the sediment-water interface. The lack of thickly graded or laminated silt sheets above these shell beds is attributed to their lying beyond the limit of transport of material eroded from the coast during the storms which gave rise to these units. They are therefore considered to originate from the passage of distal, relatively low energy, storm swells. The shell beds of group 1 being their more proximal, high energy, contemporaries, involving more current action, erosion and transport of material.

Similar shell concentrations have been recorded from the N. Atlantic Holocene (Powers & Kinsman 1953), the Jurassic of Wyoming and Montana (Brenner & Davies 1973), the Upper Muschelkalk of S.W. Germany (Aigner et al. 1978; Aigner 1979) and the Ludlovian of the Welsh Borderland (Watkins 1979) as forming in the same way, lateral transport being only a few metres at the most. The marked similarity of the faunas in the group 2 shell beds compared to the surrounding sediments suggests this was also true for the Lower Bringewoodian.

Lower Bringewood Beds - Facies 2 - The Nodular Bioturbated Siltstone Facies

This is found forming a minor thickness of the Lower Bringewood Beds at Leintwardine, Ludlow, Perton and the River Onny. It is almost identical in many respects to the bioturbated siltstone facies described above. However, it is more calcareous, shell fragments are more abundant and calcareous nodules are extremely common. These nodules occur both randomly through the sediment and in courses, where nodules may be seen coalescing; they are semielliptical to semispherical in shape with their longest axes between 4 and 20 cm long and parallel to bedding. Cross bedding is present in this lithology.

Interbedded with this lithology at Ludlow are group 2 shell beds (whose formation was discussed during the analysis of the above facies). Interpretation. These beds were deposited in a more turbulent environment than those of the bioturbated siltstone facies. They show that short lived more turbulent periods existed during the deposition of the Lower Bringewoodian sediments. Similar variations in turbulence are known from the Upper Bringewoodian (Newall 1966).

Upper Bringewood Beds - Facies 1 - The 'Aymestry Limestone' Facies

This facies forms the complete thickness of the Upper Bringewood Beds in all the sections examined in the present study except the Bengry Track (Aymestrey) and the Brookend borehole. The following description is based on this author's examinations and a review of the published literature on each of the shelf areas that have been mapped (p.2).

The Aymestry Limestone is a series of olive grey, silty, nodular limestone beds which have thin shale partings (a few centimetres thick) every several metres or so up the succession. In fresh sections (e.g. Woodbury Quarry) the limestone appears massive but on weathering it quickly breaks down to a mass of calcareous nodules set in an extremely calcareous siltstone matrix.

The nodules are ellipsoidal to subspherical in shape and occur in large numbers throughout this facies. The nodules are often seen as courses and neighbouring nodules may coalesce to give odd shapes. Individual nodules generally have their longest axes between 4 and 20 cm long, and parallel to bedding. These nodules are composed almost entirely out of microsparite or micrite with very rare grains of quartz, mica or bioclasts. Occasionally bryozoa are found encrusting the surface of these nodules. This suggests that these nodules, unlike those of the Upper Eltonian or Lower Bringewoodian may have been reworked or have formed local 'microhardgrounds'.

In polished section the sediment enclosing the nodules is seen to show a complex mottling, identical to that seen in the bioturbated siltstone facies and interpreted as originating from extensive bioturbation; a considerable amount of shell debris is also apparent. In thin section these sediments are seen to differ from the bioturbated siltstone, in that they contain less clay, more and larger sized quartz and considerably more shell debris and fragments. These features suggest that they were deposited in more turbulent conditions than any previously described facies.

The fauna of these beds often shows disarticulation, some fragmentation, the more delicate features of the shells are often broken or damaged and shell imbrication is quite common. These features suggest some transportation may have taken place in this more turbulent environment.

The Aymestry Limestone facies always shows the above features but other features may be present or absent depending on which area it is being examined. It is possible to separate the Aymestry Limestone of the shelf edge region (at Leintwardine, Ludlow, the River Onny and east of the Bengry Track at Aymestrey) from that of the rest of the shelf.

1) The shelf edge region limestone contains abundant poorly sorted rounded bioclasts. Current bedding, scours, channelling and imbricated fossils are quite common. Their most striking feature,

however, is the presence of bands containing abundant closely packed Kirkidium valves or tabulate coral colonies. Newall (1966) studied the palaeoecology and sedimentology of the Aymestry Limestone especially in this region and on faunal and sedimentological evidence was able to identify three units within the limestone. The Kirkidium Units with abundant almost monospecific occurrences of this brachiopod were considered to represent a very high energy environment, possibly within the breaker zone; although many of the shells were disarticulated he concluded that they had not moved far from their life position. The Coral Units containing an abundance of compound tabulate corals, mostly in growth position, were thought to have grown in the shallow photic zone under conditions of fairly high turbulence (but not as great as the Kirkidium Units). Finally the Atrypa-Strophonella Units which were considered to have developed in the least turbulent environments, both compound corals and Kirkidium are rare in these beds while A. reticularis and S. euglypha are both common. From sedimentological work Newall (1966) concluded that the Aymestry Limestone developed in response to increased turbulence in the depositional environment, the underlying siltstone (the Lower Bringewood Beds) being deposited in relatively quiet water and as turbulence increased so the limestone developed. The Kirkidium Units were established during periods of maximum turbulence and as turbulence decreased first Coral Units and then Atrypa-Strophonella Units developed. These shelf edge deposits of the Aymestry Limestone are thought to represent a barrier established possibly as a submarine ridge (Alexander 1936; Lawson 1973a; Watkins 1979) which may have been covered by only very shallow water. The presence of green algae at Aymestrey was taken by Lawson (1973a) to indicate depths of water of less than 30 m. However, Riding (1975) indicated that calcified green algae may inhabit depths up to 100 m. Although the alga found by Lawson is non-calcified (Elliott 1971) Riding's comments indicate care must be taken in using algae as depth indicators. There seems no doubt, however, that these Upper Bringewoodian strata were deposited in quite shallow water.

2) The Aymestry Limestone at Millichope, Woodbury, Perton and Usk is noticeably more silty and less calcareous (although it is still more calcareous than any other facies). Scouring, channels and cross bedding are much rarer. The Kirkidium and Coral Units are missing and the beds resemble the Atrypa-Strophonella Units most closely in both fauna and lithology. All these factors suggest a less turbulent

environment than at the shelf edge barrier deposits, but still more turbulent than any other considered so far. Mohamed & Tucker who are investigating the sedimentology of the Upper Bringewoodian agree that these deposits accumulated in a shallow marine environment (pers. comm. 1977 & 1978).

Upper Bringewood Beds - Facies 2 - The Silty 'Aymestry Limestone' Facies

This facies comprises the Upper Bringewood Beds of the Bengry Track (Aymestrey) and the Brookend borehole and the lowermost Upper Bringewood Beds at Woodbury. Lithologically similar to the above facies but with significantly more silt and less calcareous material. Calcareous nodules are less common and shell debris is rarer than in the above facies but commoner than in any underlying facies. These deposits are an extension of the trend towards more silty and less calcareous deposits away from the shelf edge, both towards the inner shelf and out into the basin. The presence of cross bedding, abundant shell debris and disarticulated and imbricated shells all suggest a fairly turbulent environment and Farrow (in Lawson 1973a) suggested that this material was probably deposited above wave base.

Conclusions Of Sedimentological Investigations

Upper Elton Beds. During the Upper Eltonian, over the whole shelf area, low energy conditions prevailed, in this distal environment fine material settled out of suspension. The lack of storm deposits indicates that the area lay beyond the reach of such activity. The rarity of bioturbation and trace fossils in most of these beds is considered to indicate less than fully oxygenated bottom conditions, due to low turbulence and therefore poor mixing of the water. Well away from the shelf edge at Usk bioturbation is seen to be commoner and in the Brookend borehole the sediments are completely bioturbated, indicating an increase in oxygenation of the bottom, probably due to increased turbulence producing more complete mixing of the water.

Lower Bringewood Beds. Due to a major increase in turbulence the bottom waters of the whole shelf became better oxygenated and therefore benthic organisms were able to burrow into and completely rework the sediment over the entire shelf. Since normal sedimentation on the shelf was the slow settling out, from suspension, of silt and clay to form the bioturbated siltstone facies. Although this facies is remarkably similar across the shelf there does appear to be an increase in the proportion of quartz and shell debris and fragmentation, and a

decrease in the proportion of clay away from the shelf edge. This is interpreted as a gradient from quieter, distal sedimentation at the shelf edge, where bottom waters may still have been less than fully oxygenated to a more proximal environment in the shelf inliers area, with higher energy more turbulent conditions prevailing. Occasionally quite turbulent conditions prevailed, documented by the development of a more nodular and calcareous lithology, the nodular bioturbated siltstone facies. The faunal assemblages from these deposits (and the Upper Eltonian) are analogous to the disturbed neighbourhood assemblages of Scott (1974) in that, although the fauna may not be preserved in its life position, it has probably not moved far from it.

During storms, in the proximal areas shells and sediment were swept into suspension by waves which eroded the top surface of the sediment. The shells were transported in clouds of silt and settled out of suspension as shell layers as the current depleted. Over these was deposited material, silt and sand, eroded from nearshore areas and carried out to sea by retreating waves as suspension clouds eventually being deposited with a decrease in energy either as graded or laminated units. In more distal areas, nearer the shelf edge, storm generated swells suspended shells and the topmost sediment layer which after the swell had passed settled back to the bottom with little lateral transportation of shells. In areas very close to the shelf edge, storm deposits are very rare and this must be very close to the limit of storm influence.

Upper Bringewood Beds. A further major increase of turbulence in the depositional environment led to the formation of the most calcareous phase of the Ludlovian. Deposition over the whole shelf during this time was probably in quite shallow water and above wave base. However, the highest energy, most turbulent conditions now existed at the shelf edge where a barrier was set up and turbulence decreased to the south-east (a reversal of the previous trend due to the protection afforded by the shelf edge barrier) and to the west, towards the basin where siltier, quiet water deposits accumulated.

CONTINUOUS REGRESSION IN THE LUDLOVIAN?

The major increases in the energy and turbulence of the depositional environment at the base of the Lower Bringewoodian and Upper Bringewoodian are thought to reflect a shallowing trend which reached its maximum in the shallow water high energy environment of the Upper Bringe-

woodian, and was followed by a transgression at the base of the overlying Lower Leintwardinian, as proposed by Phipps & Reeve (1967) for the Malvern area. Calef & Hancock (1974), however, considered that they had found no evidence of cyclic transgressions and regressions during their study of Ludlow 'communities' and assumed continuous regression throughout the Ludlovian. This view has been reiterated by McKerrow (1979) and Watkins (1979). Although the latter examined the Upper Bringewoodian sediments, unlike Calef & Hancock or McKerrow, he considered that, apart from the shelf edge deposits, they were deposited in deeper water than the overlying Lower Leintwardinian. Lawson (1975) has refuted this idea on both sedimentological and faunal grounds. R. Marsh (1976) carried out chemical analyses of sediments throughout the Ludlovian of the Welsh Borderlands and concluded that marked changes in the mineralogy, especially of the clay minerals, supported the model of Phipps & Reeve (1967). Cherns (1977) provided evidence of a marked transgression at the base of the Lower Leintwardinian on the shelf, since her sedimentological work showed them to be deposited well below wave base, yet parts of the Upper Bringewoodian were deposited in the breaker zone and the whole of this latter division appears to have been deposited above wave base. Therefore continuous regression throughout the shelf facies Ludlovian seems untenable.

SHELF FAUNA

During this study over 68,000 individual fossils representing about 90 species were extracted from the two Lower Bringewoodian shelf facies.

Comparisons of Lower Bringewoodian faunas between sections was aided by calculating the 'mean relative abundance' of each taxon for transported and disturbed neighbourhood assemblages in both Lower Bringewoodian shelf facies in all the 9 shelf sections examined. The 'mean relative abundance' of a taxon is the mean relative abundance percentage of that taxon in all collections from a given category (e.g. disturbed neighbourhood assemblages of the bioturbated siltstone facies) in any one section. This data is presented in Table 3.2 (for the bioturbated siltstone facies) and Table 3.3 (for the nodular bioturbated siltstone facies).

Comparing the mean relative abundances of taxa in the disturbed neighbourhood and transported assemblages in one lithology in one section indicates the degree to which the fauna of the transported assemblages

is depleted or enriched in various taxa relative to the disturbed neighbourhood assemblages in the surrounding sediments. This gives some indication of the extent to which taxa of the transported assemblages have been transported.

Mean relative abundances can also be used to examine lateral faunal changes in shelf sediments by comparing the values of a taxon in the disturbed neighbourhood assemblages (not the sorted and transported fauna of the shell beds) of different sections for any one facies. By arranging these sections in order of increasing distance from the shelf edge and comparing the mean relative abundances for each taxon (in the same facies), lateral changes in the shelf fauna within one facies become apparent (e.g. Table 3.2; Fig. 3.12).

However the shelf fauna changes vertically as well as laterally in any one facies (e.g. the upward decrease of S. ludloviensis in the bioturbated siltstone facies at Woodbury, Fig. 3.7). Although an examination of vertical and lateral faunal changes in disturbed neighbourhood assemblages of the shelf sediments reveals the latter to be more marked than the former for any one facies, i.e. variation in geographical distribution is more pronounced than sequential changes through time at any one locality.

By examining both lateral (see Tables 3.2, 3.3; Fig. 3.12) and vertical (see Figs. 3.2 to 3.10) changes in the composition of the disturbed neighbourhood assemblages in the shelf sediments the distribution of the shelf fauna (relatively unmodified by transport) can be considered.

Distribution Of Individual Taxa (Untransported)

As noted above, the distribution data is derived from the disturbed neighbourhood assemblages, since these are considered to be fairly close to the original faunal distribution. An attempt is made to explain the distribution of each taxon using data on the palaeoenvironment, as derived from sedimentological studies, and the autecology of each form, as deduced from functional morphology.

In this section the distributions of fossil taxa are outlined in a brief prose description; this is not meant to accurately describe the distribution of each species, since this is given in the tables and figures presented in this chapter, but rather to emphasise the main aspects.

So that the fauna of the Lower Bringewoodian may be considered in context data is included on the Upper Eltonian and Upper Bringewoodian faunas; this is taken from this author's observations and the work of

Table 3.2 Mean relative abundance values for the disturbed neighbourhood assemblages and transported assemblages (figures in brackets) of the Lower Bringewoodian bioturbated siltstone facies

	LEINTW-ARDINE	RIVER CONNY	LUDLOW		PERTON
A.grayi		2.00			
A.funiculata	0.23	0.23	1.02		1.80
A.reticularis	15.18	15.67	37.31	(28.00)	29.20
C.implicata		0.53	0.63		1.15
dalmanellids indet.	0.23		0.05		
E.radiatus	0.90		0.59		
G.galeata	0.95		0.63		1.85
G.lata	23.75	8.03	5.55		2.65
H.elegans		0.73	1.70		
I.orbicularis		8.43	5.82	(4.00)	13.50
K.knightii	0.23		0.10		
L.depressa	2.78	0.30	4.14		1.75
L.filosa		1.40	0.19		0.85
L.lewisii	0.23	0.40	1.40		0.25
Lingula sp. A			0.04		
M.cf.lepisma	0.45	9.93	4.37	(10.00)	6.25
M.nucula			1.13	(2.00)	
P.ludloviensis					1.40
P.minimus					0.95
S.ludloviensis	35.48	19.93	7.47	(50.00)	7.00
Shaleria sp. nov.		0.23	0.21		
S.wilsoni	0.48	2.13	3.84		3.40
S.euglypha	5.23	6.33	8.83		3.15
A.pleuroptera			1.05		
C.cornucopiae			0.13		
C.planulata	0.45		0.38		0.25
C.subplanulata			0.15		
G.cymbaeformis			0.18		
Modiolopsis sp.			0.05		
N.antiquus			0.07		
O.nasuta			0.08		
?Paracyclus sp.			0.21		
Pteronitella sp.			0.17		
bivalve indet.			0.18		
D.myops	1.40	1.83	0.81		1.20
E.rosensteinae		0.23			
P.astringens					0.30
beyrichiaceans			0.07		
smooth ostracods	0.45	1.43	0.20		7.00
Ceramopora sp.			0.10		
dendroid trepostome	0.23		1.80		1.80
encrusting trepostome		0.17	1.20		1.10
Fistulipora sp.		1.47	1.05		0.25
P.lanceolata		0.33	0.28	(2.00)	1.10
vinculariiform trepostome	3.35	15.07	0.41	(2.00)	10.15
L.striatissima			0.49		
L.obsoletum		0.30	0.25		
P.globosa		1.30	0.58		0.95
Favosites sp.	1.13		0.64		
R.porpitoides	1.60	0.17	2.07		
small horn corals	0.65		0.49		
solitary coral sp. B	0.88		0.17		0.30
'Cyrtoceras' sp.			0.09		
K.angulatum		0.40	0.27		
M.bullatum	0.23		0.03		
P.tumescens	1.63	0.47			
S.clunensis	1.13		0.04		
T.ornatus					0.25
tentaculites sp.			0.07		
crinoid ossicles (round)	0.68	0.53	1.26		
TOTAL %	99.93	99.97	100.04	(100.00)	99.80
TOTAL NUMBER OF SPECIES	26	28	53	(8)	27
NUMBER OF SAMPLES	4	3	15	(1)	2
AVERAGE DENSITY	20.1	57.6	20.2	(625.0)	35.9
AVERAGE SP. PER COLLECTION	13.5	18.3	16.0	(8.0)	22.0
AVERAGE SP. PER 100 INDIV.	13.0	16.4	18.9	(-)	19.7

Table 3.3 Mean relative abundance values for the disturbed neighbourhood assemblages and transported assemblages (figures in brackets) of the Lower Bringewoodian nodular bioturbated siltstone facies

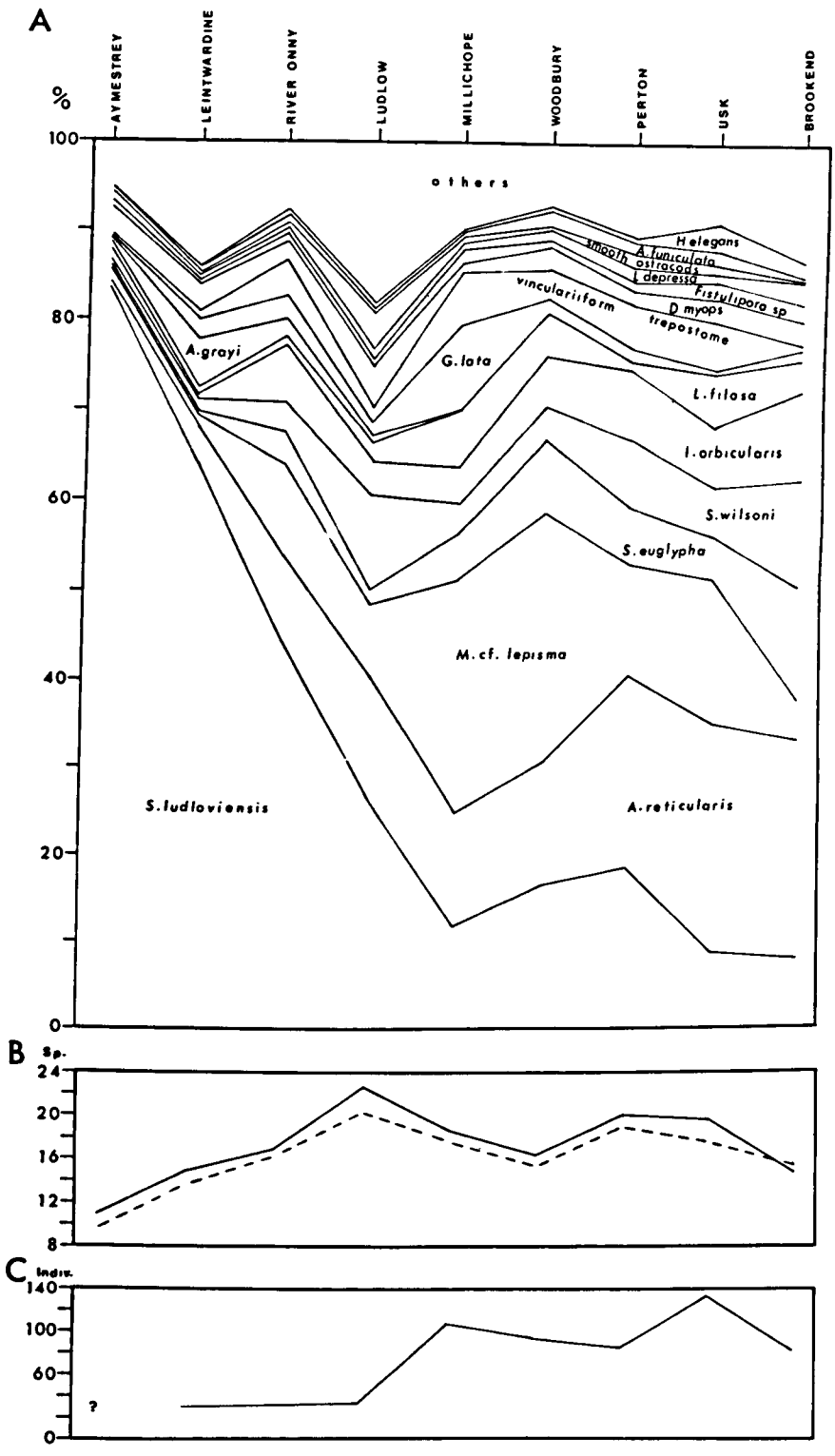

Fig. 3.12 A) Mean relative abundance (%) values for the commonest species in the disturbed neighbourhood assemblages of the bioturbated siltstone facies (the dominant Lower Bringewoodian facies of the shelf) in each shelf section examined B) Mean diversity values for the above assemblages , solid line indicates the mean number of species per collection in each section , broken line represents the mean number of species per 100 individuals in each section C) Mean density values for the above assemblages , mean number of individuals per 5000 cm^3 of sediment in each section. Sections are arranged in order of increasing distance from the shelf edge (Aymestrey to Brookend) and are shown a standard distance apart.

Walmsley (1959), Squirrell & Tucker (1960), Whitaker (1962), Holland et al. (1963), Phipps & Reeve (1967), Shergold & Shirley (1968), Lawson (1973a) and Cave & White (1978).

S. ludloviensis. This form is extremely abundant in the topmost Upper Eltonian and in the bioturbated siltstone facies of the Lower Bringewoodian of the shelf edge region where it forms between 60% and 80% of the entire fauna and dominates in almost every collection. Away from the shelf edge area, however, its abundance declines rapidly and almost continuously so that in the inner shelf areas of Usk and Brookend it forms less than 10% of the bioturbated siltstone facies fauna. It is uncommon to moderately common in the nodular bioturbated siltstone facies. S. ludloviensis decreases in abundance in some sections as the Upper Bringewood Beds, in which it is virtually absent, are approached. This distribution reflects a preference for quiet water environments to which this species was well adapted (p.10) and an intolerance of turbulence. The light, thin, unattached shells would have been easily swept away in high energy conditions to which they are not adapted. They are, however, due to their small size, well adapted to conditions of poor water circulation and therefore possibly below normal levels of food and oxygen (p.10) which appear to have existed in the quiet waters of the Upper Elton Beds and possibly also in the outermost shelf of the Lower Bringewoodian bioturbated siltstone facies.

A. reticularis. This species is virtually absent from the Upper Eltonian and is rare in the shelf edge region of the bioturbated siltstone facies although it increases in abundance rapidly and continuously to become the commonest fossil in the inner shelf region of this facies. It is also very common in the nodular bioturbated siltstone facies and in the Upper Bringewood Beds where it is one of the commonest species. This distribution appears to indicate an intolerance of quiet conditions and a preference for more turbulent environments. It is significant that many specimens from the shelf edge area show flanges which appear to be absent from most specimens in the inner shelf areas; this may indicate that the substrate of the outer shelf areas was softer and muddier resulting in the development of flanges on the species to support it (see p.11). One of the most noticeable features about A. reticularis is the increase in both the mean size and the largest size to which the shell grew in populations from the shelf edge to the inner shelf. This is shown in Fig. 3.13, 9 populations of A. reticularis were examined,

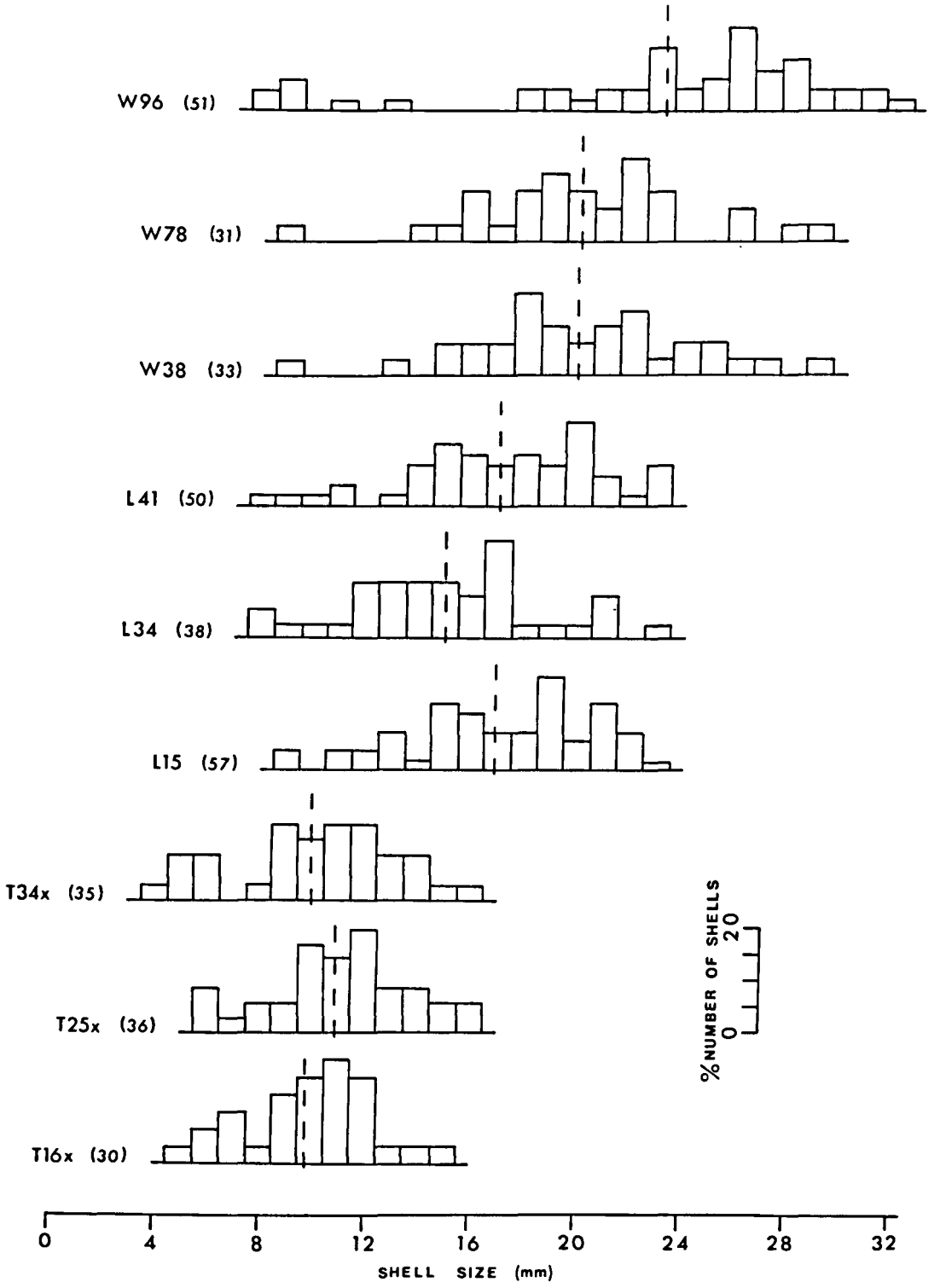

Fig. 3.13 Size frequency histograms , showing mean size (vertical bars) for 9 populations of Atrypa reticularis from 3 localities , Woodbury (W) , Ludlow (L) and Leintwardine (T) , in the bioturbated siltstone facies of the Lower Bringewoodian. Shell size is measured as (length + width) / 2 . Histograms standardised to 100 individuals to aid comparison ; actual number of shells in each sample are given in parentheses.

3 from each of the sections at Leintwardine, Ludlow and Woodbury. Due to the rarity of this species at Leintwardine these collections were not part of the ordinary collecting but were made separately. They all come from the bioturbated siltstone facies and none are from transported shell beds. The close packing of growth lines at the valve margins of the largest shells in all these populations indicates that maturity had been reached (Hallam 1965, p.141; Worsley & Broadhurst, 1975, p.284) despite the small size of the Leintwardine specimens which therefore appear to be stunted. A. reticularis therefore appears to have required moderate turbulence (to which it was well adapted) to thrive, while in quieter waters it becomes rare and stunted. Other authors have come to similar conclusions (p.12).

M. cf. lepisma. This species is almost absent from the Upper Eltonian. It is rare in the bioturbated siltstone facies of the shelf edge area but becomes commoner away from it, becoming the most abundant taxon in the middle shelf region around Millichope and Woodbury. However it declines in abundance towards the inner shelf so that it is only moderately common at Brookend. The nodular bioturbated siltstone facies contains only moderate numbers of M. cf. lepisma and it is virtually absent from the Upper Bringewood Beds. This distribution reflects the adaptation of this species to moderately turbulent environments (p.13).

S. euglypha. This species is absent from the Upper Elton Beds except in the Brookend facies. In the bioturbated siltstone facies S. euglypha is rare in the outer shelf, moderately common in the middle shelf and common in the inner shelf. In the nodular bioturbated siltstone facies S. euglypha is common. It is one of the commonest fossils of the Upper Bringewood Beds. This distribution suggests a preference for turbulent conditions to which this large, thick, heavy shell is well adapted (p.14).

S. wilsoni. This species occurs very rarely in the Upper Elton Beds. It is fairly common in most sections through the Lower Bringewoodian, except at the shelf edge; its abundance increases away from this area. It is moderately common in the Upper Bringewood Beds. S. wilsoni therefore appears to have preferred relatively turbulent environments to which it was well adapted (p.15). It may well have lived pedically attached to algal fronds in such environments (p.16).

I. orbicularis. Rare in the Upper Elton Beds this species becomes quite common in the Lower Bringewoodian. In the bioturbated siltstone facies

it is common in the inner shelf region but becomes less common towards the shelf edge where it is rare. It is common in the nodular bioturbated siltstone facies and the Upper Bringewoodian. An intolerance of quiet water environments again appears to be indicated by this distribution. This pedically attached form appears to be quite well adapted to moderately turbulent environments (p.18).

L. filosa. Absent from the Upper Elton Beds this species is quite common in the bioturbated siltstone facies of the inner shelf area, although it is rare in this facies in the shelf edge region. It is also rare in the nodular bioturbated siltstone facies and the Upper Bringewoodian. It appears to have preferred moderately turbulent waters, a fact explicable by its lack of adaptations to either very quiet or very turbulent conditions (p.14).

Gypidulids. G. galeata is absent from the Upper Elton Beds and rare throughout both facies of the Lower Bringewood Beds. G. lata is absent from the Upper Elton Beds. In the Lower Bringewoodian bioturbated siltstone facies it is rare in the shelf edge and inner shelf areas but is common in the middle shelf area especially around Millichope. G. lata is more common in the nodular bioturbated siltstone facies and is fairly common in the Upper Bringewoodian. Gypidulids were not adapted to either quiet water or high energy conditions but to the moderately turbulent environments between these two extremes (p.17). The distribution noted above agrees with such an interpretation. G. lata appears to have been more successful than G. galeata.

A. grayi. This species is confined to the Upper Elton Beds and the outer shelf area in the bioturbated siltstone facies. It is rare in the nodular bioturbated siltstone facies and absent from the Upper Bringewoodian. At Leintwardine in the bioturbated silt facies A. grayi is abundant in three collections (T7, T8 and T13) which show no lithological differences from other collections which are dominated by S. ludloviensis. The occurrence and functional morphology of A. grayi led to the conclusion (p.22) that it may have been either benthic (attached to benthic algae or floating algae which had sunk) or epiplanktic. The abundance of A. grayi in the three collections at Leintwardine may suggest an opportunistic benthic species (Levinton 1970) or they may represent epiplanktic assemblages which were attached to floating algae which had sunk. It is not possible from this evidence to decide which is the case. The absence of this species from turbulent

environments is either because they were benthic and could not adapt to such high energy conditions, in which their small light shells would be easily broken up, or, alternatively they were epiplanktic and all their shells which fell into turbulent waters were destroyed; a further possibility is that the species was epiplanktic but confined to surface waters above low energy environments.

P. minimus. Present in the Upper Eltonian, this species occurs rarely but consistently right across the shelf in the bioturbated siltstone facies. It is rare in the nodular bioturbated siltstone facies and absent from the Upper Bringewoodian. Such a distribution suggests a preference for quiet water conditions to which the shell was best adapted (p.19).

L. depressa and E. radiatus. Both these species are absent from the Upper Elton Beds, they are rare in the bioturbated siltstone facies, commoner in the nodular bioturbated siltstone facies and quite common in the Upper Bringewood Beds. This distribution suggests a preference for turbulent conditions to which these large heavy shells are well adapted (p.14-15, 22).

P. ludloviensis and M. nucula. Both these species are absent from the Upper Elton Beds. They are extremely rare or absent in the shelf edge region and uncommon in the inner shelf areas in the Lower Bringewoodian and the Upper Bringewood Beds. The very low abundance of these species suggests that conditions were less than ideal at this time. Their appearance in the more turbulent environments however is explicable by their adaptations to shallow nearshore environments (p.16, 19). M. nucula may have been attached to benthic algae (p.16).

H. elegans. This species is absent from the Upper Elton Beds, rare in the bioturbated facies of the shelf edge, uncommon in the inner shelf areas of the latter facies and in the nodular bioturbated siltstone facies and quite common in the Upper Bringewoodian. Clearly this distribution reflects a preference for turbulent high energy conditions to which the shell is well adapted (p.20).

A. funiculata. This species is absent from the Upper Eltonian, present but uncommon in the Lower Bringewoodian, and very rare in the Upper Bringewoodian. This distribution reflects a preference for moderate energy environments (neither very quiet or very turbulent) to which this shell is well adapted (p.15).

Shaleria sp. nov. and C. pecten. These species are rare to uncommon throughout the entire Lower Bringewoodian; they are absent from the underlying and overlying beds. This distribution reflects their lack of adaptation to either high or very low energy conditions (p.22).

K. knightii. This species is absent from the Upper Elton Beds and is recorded here from the Lower Bringewoodian for the first time (it occurs extremely rarely in the bioturbated siltstone facies of Leintwardine and Ludlow and slightly less rarely in the nodular bioturbated siltstone facies). K. knightii is common in the Upper Bringewoodian, especially in the Kirkidium bands of the outer shelf area. This distribution reflects a preference for very high energy conditions, to which the shell is well adapted and an apparent requirement for clear water (p.21).

D. navicula. This species is present rarely in the Upper Eltonian but is almost totally absent from the Lower Bringewoodian shelf sediments in which it occurs only in the bioturbated siltstone facies of the outermost shelf. It is absent from the Upper Bringewoodian. This distribution reflects the species' adaptation to very distal quiet water conditions (p.20).

Lingulids. All three species from the Lower Bringewoodian have been found as articulated valves disposed normal to bedding, mostly anterior upwards and therefore apparently they lived in burrows. During the Upper Eltonian L. lata was confined to the outer shelf sediments and L. lewisii was confined to the inner shelf. In the Lower Bringewoodian L. lata was confined to the very outermost shelf area (and the basin, see Chapter 4) where it occurs in the lowermost strata of this division together with L. lewisii which is found rarely but consistently throughout the Lower Bringewoodian shelf sediments. The extremely rare Lingula sp. A occurs sporadically throughout the Lower Bringewoodian shelf sediments. L. lewisii is present in the Upper Bringewoodian of the shelf. L. lata therefore appears to have been restricted to areas of probably less than fully oxygenated bottom waters which may have been turbid, to which it was apparently well adapted (p.24). However, L. lewisii appears to have been confined to better oxygenated waters, being unable to stand such basinal-like conditions (p.24). The distribution of the two species overlap only at the extremes of their respective tolerances. It is notable that L. lewisii is distinctly larger in the inner shelf than outer shelf sediments in the Lower Bringewoodian, suggesting a more favourable environment in the inner shelf. Cherns (1977) made similar observations in the Lower Leintwardinian.

O. rugata and C. implicata. Both species are rare throughout the Upper Eltonian and Bringewoodian; conditions therefore were not very favourable for them.

Bivalves. Considering their low abundance bivalves show a remarkable diversity (16 species) in Lower Bringewoodian shelf sediments. All of these species (recovered during this study) are rare and the bivalves of the bioturbated siltstone facies make up less than 1% of the total fauna in all sections except the River Onny (1.3%), Ludlow (2.6%) and Brookend (4.3%). In the bioturbated siltstone facies bivalves form less than 1% of the fauna in all sections except Ludlow (2.7%). By far the most abundant forms are endobyssate suspension feeders (9 species including C. planulata, C. subplanulata, Pteronitella sp. and G. cymbaeformis). Shallow burrowing suspension feeders (O. nasuta) and deposit feeders (N. antiquus and P. ludensis) are the next commonest. Free burrowing forms (Paracyclus), epibyssate forms (P. mytilimeris) and epiplanktic forms (P. tenuistriata and C. cornucopiae), all suspension feeders, are very rare. Deposit feeders dominate soft muddy bottoms, in which the waters are turbid due to the reworking activity of these organisms (Rhoads 1970). The absence of filter feeding bivalves in such environments is due to resuspended mud clogging their filtering apparatus (Rhoads & Young, 1970; Steele-Petrović 1975). The large number (14) and relative abundance of filter feeding bivalves in the Lower Bringewoodian, suggests that the waters overlying the shelf at this time were not turbid. Stanley (1972), Watkins (1978a) and Steele-Petrović (1979) have all noted that Palaeozoic bivalves have their highest abundance where the environment exerted stresses that imposed restrictions on other species. The low abundance of bivalves in the Lower Bringewoodian suggests relatively low stress conditions. The high diversity of Lower Bringewoodian bivalves was considered by Watkins (1978a) to result from low population densities increasing isolation and therefore speciation. Stanley (1970), however, suggested that high bivalve species diversity in such stable firm environments (indicated by the relative abundance of burrowing filter feeders) resulted from the fact that such environments were easy to adapt to. This author considers both factors probably played a part in producing the high diversity of bivalves in the Lower Bringewoodian.

Bryozoans. After brachiopods bryozoans are the most abundant group in most sections through the Lower Bringewoodian shelf sediments. In the bioturbated siltstone facies they form between 2.7% and 8.5% of the

total fauna in all sections, except those of the outermost shelf edge in which they are noticeably less common. In the nodular bioturbated siltstone facies bryozoans are even commoner forming between 3.6% and 17.0% of the total fauna. Bryozoans are very rare in the Upper Eltonian and quite common in the Upper Bringewoodian. In the Lower Bringewoodian the commonest taxa of both facies in all sections were a vinculariiform trepostome species and Fistulipora sp. Other rarer forms with a more sporadic distribution include Ceramopora sp., dendroid trepostome, encrusting cystoporate, encrusting trepostome, fenestelid bryozoan and Ptylodictya lanceolata. Modern bryozoans (and presumably ancient ones too) require good water circulation, although not too much turbulence, the presence of firm substrates (e.g. shell fragments) for attachment and clear waters; most are fully marine forms (p.30). The lack of water circulation and therefore clear water in the quiet possibly not fully oxygenated, bottom waters of the Upper Eltonian, and the shelf edge area in the Lower Bringewoodian, probably accounts for the reduced bryozoan abundance in these strata. Away from the shelf edge the circulation of the Lower Bringewoodian shelf waters is thought to have been good, without too much turbulence; such clear water conditions were ideal for bryozoans and probably account for their success. The increased circulation (and turbulence) of the nodular bioturbated siltstone facies allowed more sturdy forms such as dendroid trepostomes (p.31) to increase in abundance. The high bryozoan abundance in this facies suggests turbulence was not yet high enough to have been limiting. However, the reduction of bryozoans in the Upper Bringewoodian suggests that turbulence may have become limiting; the presence of shells in all the environments recognised suggests the lack of firm substrates did not limit bryozoan colonisation.

Graptolites. In the Upper Elton Beds graptolites, particularly P. tumescens, are abundant in most sections, although they become rarer in inner shelf areas. At the base of the Lower Bringewoodian graptolites become uncommon in all shelf sections and are far less abundant than in the Upper Eltonian. In the bioturbated siltstone facies, graptolites are very rare in inner shelf areas but gradually increase in abundance towards the shelf edge area. Graptolites are less common in the nodular bioturbated siltstone facies but again there are more in the shelf edge area. The Upper Bringewood Beds yielded no graptolites during this study. Since graptoloids lived, suspended below gas filled vacuolated tissue in the uppermost water layer (p.31, 32) their density

per unit volume of sediment would be expected to stay fairly constant over the whole shelf, since the thickness of shelf sediments in most sections is similar. The decrease in graptolites, per unit volume of sediment, away from the shelf edge in the Lower Bringewoodian and their abundance in the quiet waters of the Upper Eltonian, compared to the high energy Upper Bringewoodian in which they are absent, suggests that this distribution may be a result of selective preservation as suggested by Rickards (1975) with more graptolites being broken up in more turbulent waters (p.32). Watkins & Berry (1977) suggested that the environment of the surface water mass over the shelf was unfavourable to graptolites and therefore this accounted for their distribution (p.33). However, this model does not explain why the Lower Bringewoodian should contain graptolites in all shelf sections (although they are uncommon) yet they should be absent from the Upper Bringewoodian of all shelf sections, especially when the water masses are considered to have remained stationary during the whole of the Bringewoodian (Watkins & Berry p.274-275). Watkins & Berry's failure to consider a selective preservation control also throws doubt on the validity of their conclusions. The selective preservation explanation for graptolite distribution therefore appears most likely.

Cephalopods. Small smooth orthocones are quite common in the Upper Eltonian but disappear from the shelf sediments at the base of the Lower Bringewoodian. They are found only in the basin at this level suggesting they may have been smashed up in the more turbulent shelf waters, perhaps; they were probably nektic living in the surface waters (p.34). The orthocones that occur rarely and sporadically throughout the Bringewoodian are large ornamented forms, which were probably nektobenthic (p.34). Their absence from the Upper Eltonian is possibly due to the paucity of their probable prey (benthic fauna) which may have been largely excluded by poorly oxygenated conditions. The presence of unimploded brevicones on the shelf, at Ludlow, suggests that the water depth here was less than 250 m and perhaps even less than 50 m (p.33) however, caution has been urged in the determination of depth ranges from fossil cephalopods (p.34).

Gastropods. Gastropods (5 species, all archaeogastropods, in total) are a very minor element of the Lower Bringewoodian fauna of the shelf sediments, occurring rarely and somewhat sporadically; their abundance decreases in the shelf edge area. Gastropods are equally rare in the Upper Bringewoodian and virtually absent in the Upper Eltonian. Their

virtual exclusion from the Upper Eltonian and the outermost shelf in the Lower Bringewoodian is probably due to the quiet water conditions that apparently existed resulting in poorly oxygenated and more silty, less clear waters; archaeogastropods have a requirement for clear water conditions (p.35).

Trilobites. Trilobites form a few percent of the total fauna in all sections through the Lower Bringewoodian. They are present in the Upper Bringewoodian but very rare in the Upper Eltonian. Conditions in the Upper Eltonian were obviously unsuitable for trilobites, possibly due to the quiet water, apparently insufficiently oxygenated conditions limiting them and their possibly prey (benthic fauna). It is notable that the two proetid species P. obconicus and P. astringens show a mutually exclusive distribution, the former being confined to the outer shelf while the latter characterises the inner shelf area. They both occur rarely and sporadically. Their mode of life is problematical (p.36) and there is no evidence from morphological studies for this distribution (Owens, pers. comm. 1978).

Corals. Corals are absent from the Upper Eltonian, uncommon in the Lower Bringewoodian and common (especially tabulates) in the Upper Bringewoodian. At the base of the Lower Bringewoodian corals begin to appear rarely and inconsistently but become commoner and less sporadic in the uppermost Lower Bringewood Beds. In the bioturbated siltstone facies they are most common in the innermost shelf (Brookend). Corals are slightly commoner in the nodular bioturbated siltstone facies. This distribution suggests that unfavourable conditions existed in the quieter water deposits, where circulation of water and hence food and oxygenation may have been lower than normal and the water unclear. In the more turbulent waters of the inner shelf Lower Bringewoodian and the Upper Bringewoodian circulation of water and oxygenation were much better and the water clearer, therefore corals thrived (p.37). The domed shape and absence of spherical forms in the Lower Bringewoodian suggests relatively quiet conditions and slow sedimentation (p.37) which agrees with the sedimentological evidence.

Ostracods. Ostracods are uncommon in the Upper Eltonian and the Bringewoodian. In the bioturbated siltstone facies beyrichiids appear to be commoner in the shelf edge region than the inner shelf, while the reverse is true for smooth forms. In the nodular bioturbated siltstone facies beyrichiids are very rare while smooth ostracods are common. Ludlovian

beyrichiids and smooth ostracods have been interpreted as benthic, living on algal foliage (p.37). The distribution noted above suggests smooth ostracods preferred more turbulent environments than beyrichiids. It is possible that different types of algal foliage grew in environments of different turbulence and that each of these two groups of ostracods preferred a different type of vegetation; since algae appear to influence the distribution of modern marine forms (p.37).

Crinoids. Very rare in the Upper Eltonian, crinoids occur consistently but rarely in most Bringewoodian strata. Their abundance throughout the Bringewoodian sediments is fairly constant. The Upper Eltonian waters were probably too quiet and the water circulation insufficient to supply these passive filter feeders with enough nutrients and oxygen or keep the waters clear enough for their survival (p.38).

Tentaculitids, cornulitids and Keilorites. All these taxa occur very rarely throughout the Lower Bringewoodian. Conditions were apparently less than ideal and they seem to have preferred a more proximal environment since they are all commoner in the Whitcliffe Beds.

Conclusion. By examining the sediments and functional morphology of individual taxa it has proved possible to explain the distribution of each taxon, from untransported assemblages, in terms of its adaptation to different environments, as deduced from sedimentological studies. A taxon is most abundant in the physical environment to which it was best adapted; although this may not be true in the case of transported assemblages (see below).

Transported Assemblages

The fauna of transported assemblages were not discussed in the previous section since an attempt was being made to determine the factors affecting the original, primary, distribution of the fauna. On the shelf, transported assemblages are confined to the bases of storm deposits. The relative abundances of taxa in the transported assemblages of these storm deposits, compared to those of the disturbed neighbourhood assemblages in the surrounding sediments, indicates to some extent the degree of transport to which the shells in the former type of assemblage may have been subjected.

Storm deposits from the inner shelf are inferred to have been formed in higher energy more proximal conditions than those of the outer shelf (p. 72) and the fauna reflects this with greater differences in the faunal abundance of taxa between storm deposits and the surrounding

sediment in more proximal areas (Tables 3.1, 3.2; Figs. 3.2 to 3.10). This is presumably because of greater transport and shell sorting in the higher energy, more proximal storm deposits.

For example although A. reticularis is far commoner than S. ludloviensis in the disturbed neighbourhood assemblages in the bioturbated siltstone facies at Brookend (their mean relative abundances being 24.68% and 8.11% respectively, Table 3.2) the transported assemblages from the same strata have S. ludloviensis distinctly commoner than A. reticularis (their mean relative abundances being 24.54% and 17.30% respectively, Table 3.2). Another example is that the mean abundances of the 4 commonest species in the disturbed neighbourhood assemblages of the bioturbated siltstone facies at Usk i.e. A. reticularis, M. cf. lepisma, S. ludloviensis and I. orbicularis are 26.09%, 16.07%, 8.82% and 6.64% respectively, however, in the transported assemblages from the same strata the relative abundances of these species are 35.54%, 5.42%, 2.01% and 10.56% respectively (see Table 3.2).

The absence of infaunal bivalves and lingulids from the transported assemblages is attributed to low scour of the shelf sediments during storm events (p. 66,67).

Therefore we can conclude that the recognition of transported assemblages is important, since a sample from them may give an erroneous indication of the original abundance of a taxon when it was alive.

Faunal Assemblages On The Shelf

Calef & Hancock (1974) in their work on Ludlovian 'communities' collected only 3 samples from the Lower Bringewoodian, one from each of the sections at Usk, Easthope and Ludlow. They assigned all these collections to their 'Isorthis community.' Since they assumed that each sample was typical of the whole stratigraphic division in the section from which it was taken, they assumed that the whole of the shelf during the Lower Bringewoodian was occupied by the 'Isorthis community.' They examined a maximum of 0.6 m of strata from the shelf Lower Bringewoodian (since no sample was from more than 20 cm thickness of strata) which is only 0.3% of the 215 m examined during this study. Broadly the species composition of their 'Isorthis community' is similar to that of the Lower Bringewood Bed shelf fauna described in this study, although they examined only brachiopods, but 7 genera (Dalejina, Homeospira, Glassia, Skenidioides, Meristina, Dicoelosia and Schizotreta) out of a total of 34 are unknown from this division and probably result from two samples being taken from the Elton Beds (Lawson 1975).

Lawson (1975) severely criticised the work of Calef & Hancock (1974) showing that they had assigned some faunal collections to the wrong stratigraphic divisions, that by ignoring non brachiopod benthos they had significantly altered the proportion of faunal elements in some of their 'communities', that their sampling was uneven and that their assumption that one sample was typical of the whole stratigraphic division in the section from which it was taken was incorrect. Lawson (1975) erected four benthic assemblages (including non brachiopod benthos) which correspond to each of the four Ludlovian Stages and which he argued gave a more accurate picture of the shelf faunas than Calef & Hancock's communities. This is true for the Lower Bringewoodian, the lower part of the Strophonella-Gypidula assemblage of Lawson (1975), although some species (e.g. S. ludloviensis) are definitely underestimated while others (e.g. L. depressa and D. navicula) are definitely over-estimated.

Watkins (1975, 1979) examined the Lower Bringewood Beds during a study of the whole shelf Ludlovian. He considered that two 'communities' the Mesopholidostrophia laevigata Association and the lower Sphaerirhynchia wilsoni Association existed in the Lower Bringewoodian. However, during the course of the present work it was realised that all the collections he had assigned to the latter 'community' from Lower Bringewoodian strata were in fact from the Upper Bringewoodian which he had misidentified as Lower Bringewoodian (p.53-55). Watkins's M. laevigata Association is similar in species content to the Lower Bringewoodian faunas extracted during this study but the faunal elements show remarkably different proportions. This is because Watkins (1975, 1979) considered A. grayi and S. ludloviensis (the latter being one of the commonest species in the Lower Bringewoodian) were epiplanktic and therefore because he was concerned with only benthic forms he ignored them when calculating the relative abundance of each taxon (Watkins 1975, p.49; 1979, p.211, 226). This is important because S. ludloviensis is so abundant that its omission during the calculation of relative abundances markedly alters the proportions of the remaining fauna, giving a false and very misleading picture of the Lower Bringewoodian fauna. It is very unlikely that S. ludloviensis was anything but benthic (p.10).

Therefore up to the present work only one community or assemblage had been described from the shelf Lower Bringewoodian, whose fauna was therefore considered to be fairly homogeneous both laterally and vertically through the strata. By comprehensively examining

and quantitatively recording the faunal distribution in the Lower Bringewoodian it has been shown that considerable lateral and some vertical faunal changes, particularly the abundance of the commonest species, exists. Therefore the suggestion of a homogeneous faunal assemblage for the whole of the shelf in the Lower Bringewoodian is a huge oversimplification. The lumping of many fossil collections together as one community or assemblage for the whole of the Lower Bringewoodian, as in past work, masks a more complex picture of the faunal distribution which it is possible to establish by careful collecting and analysis of the data. By examining the sediments and the functional morphology of individual taxa it has proved possible to explain the distribution of fauna in terms of their adaptation to different environments as deduced from sedimentological studies.

Although the procedure outlined above is considered essential for attempting to explain the distribution of taxa in a stratigraphical unit, further valuable information may be gained by recognising the existence of faunal assemblages. Information on such assemblages, found in the shelf area of the beds examined in this study are given below. The descriptions are necessarily very general ones, since some of the assemblages continuously grade into one another (Figs. 3.12 & 3.14). It is vital to remember that such assemblages are part of a continuum, since classification into discrete units can obscure important characteristics of the ecosystem (Johnson 1970; Cisne & Rabe 1978). Data for the descriptions below is derived from disturbed neighbourhood assemblages (which are considered to be closest in composition to the original faunas) and not transported assemblages. Descriptions of the Upper Eltonian and Upper Bringewoodian faunas refer only to the very topmost and lowermost parts of these divisions respectively, i.e. those strata examined during this study; they are rather less detailed, since they are mainly for comparative purposes. Density is given as the mean number of individuals per 5000 cm^3 and diversity as the mean number of species that would be found in a collection of 100 individuals for that assemblage.

Upper Elton Beds. The fauna is composed dominantly of graptolites and orthocones, together with small, unattached, thin shelled brachiopods. Moving from distal to more proximal shelf sediments graptolites and orthocones lose their dominance to the latter group. Faunal density is low in both distal (5 to 15) and more proximal (about 30) areas. Diversity is low and averages about 10 in all sections.

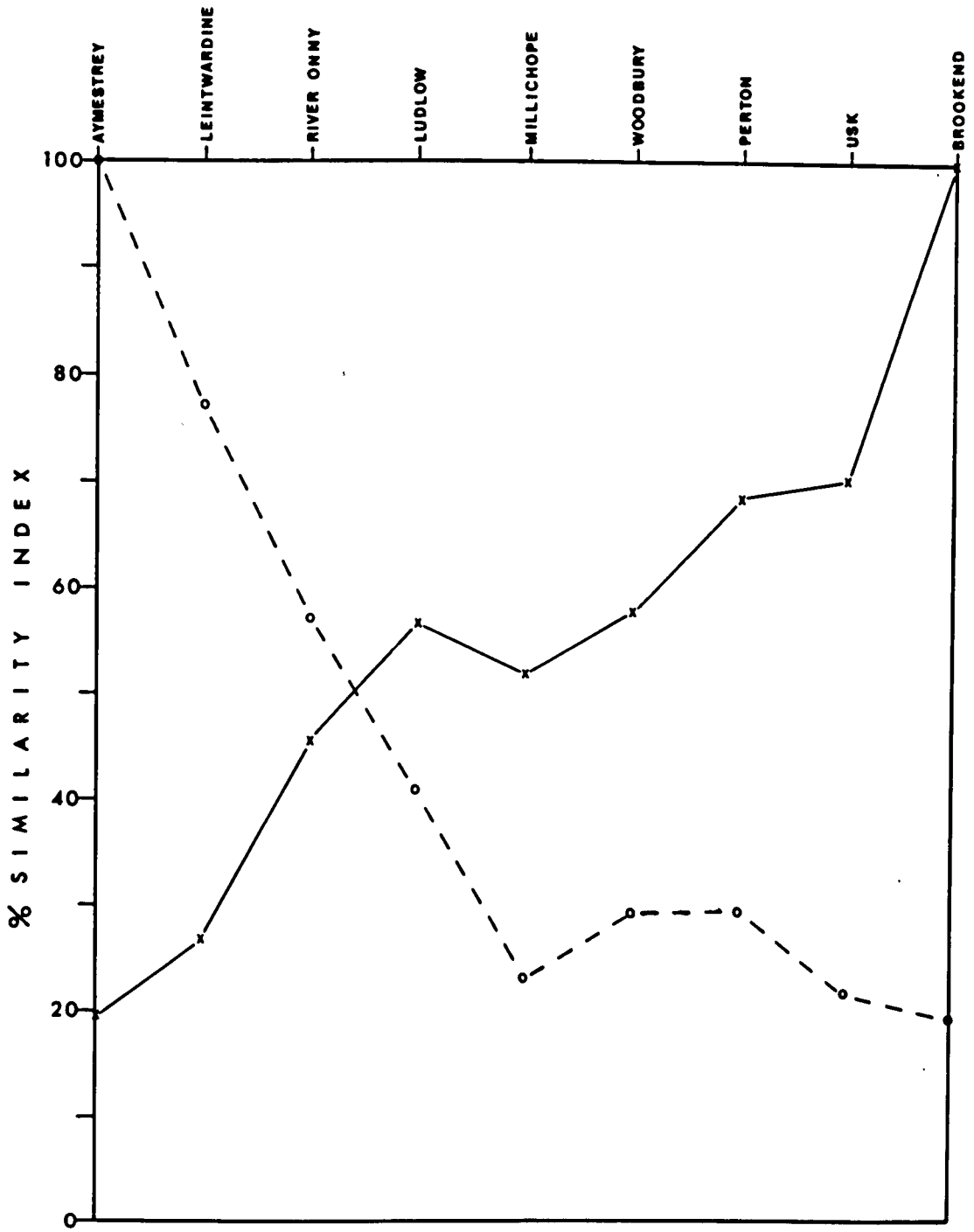

Fig. 3.14 Plots of (%) faunal similarity index (Murray & Wright 1974, p.3) values between the fauna of each shelf section and that at Aymestrey (o— —o) and also the fauna of each shelf section and that at Brookend (x——x) for the commonest lower Bringewoodian shelf facies - the bioturbated siltstone facies (disturbed neighbourhood assemblages). The overall trend is a gradual fall in values from either end member, which reflects the progressively diverging nature of faunal assemblages across the shelf. Sections are arranged in order of increasing distance from the shelf edge (Aymestrey to Brookend) and are shown a standard distance apart.

Lower Bringewood Beds. At the base of this unit there is an increase in diversity and strophomenid brachiopods become common. Groups rare or absent in the Upper Eltonian, now entering the fauna are corals, bryozoans, crinoids, gastropods and many species of brachiopods and bivalves. In the bioturbated siltstone facies 3 assemblages are recognised, although, they continuously grade into one another (Figs. 3.12 & 3.14) so that separating this faunal continuum into groups is totally artificial. Shelf assemblage 1 is an 'outer shelf' assemblage compiled from the Aymestrey, Leintwardine and River Onny areas. Small, smooth, unattached, thin shelled brachiopods, especially S. ludloviensis, dominate the fauna. Density (about 30) and diversity (10 to 16) are both low. Shelf assemblage 2 is a 'middle shelf' assemblage, compiled from the Ludlow, Millichope and Woodbury areas. S. ludloviensis is distinctly less common, M. cf. lepisma is now very common and other large unattached brachiopods have increased in importance e.g. G. lata, S. euglypha etc. Density is moderate (30 to 100) and diversity is high (16 to 20). Shelf assemblage 3 is an 'inner shelf' assemblage compiled from the Perton, Usk and Brookend areas. It is dominated by large, thick shelled, strongly ribbed brachiopods (e.g. A. reticularis) many of which were pedically attached (e.g. S. wilsoni). S. ludloviensis and M. cf. lepisma are much less common. Density is high (80 to 140) and diversity quite high (15 to 19). Shelf assemblage 4 is the fauna of the nodular bioturbated siltstone facies. Thick shelled brachiopods e.g. A. reticularis, S. euglypha, G. lata etc. are all very common. Bryozoans and corals are relatively more abundant. Density is fairly low (20 to 60) and diversity moderate (13 to 19). All 4 shelf assemblages from the Lower Bringewoodian are illustrated in Fig. 3.15.

Upper Bringewood Beds. The fauna is dominated by thick shelled, robust forms e.g. A. reticularis, S. euglypha etc. Many forms from the Lower Bringewoodian are now very rare or absent. Density is low to moderate (5 to 100) and diversity also variable but moderate (about 15).

Factors Controlling Faunal Distribution On The Shelf

Calef & Hancock (1974) statistically described five 'communities' from the Wenlock and Ludlow, of these four were considered to be well developed in the Ludlovian. The Salopina, Sphaerirhynchia, Isorthis and Dicoelosia 'communities' were considered to correspond respectively with the Eocoelia, Pentamerus, Stricklandia and Clorinda 'communities' of the upper Llandovery described by Ziegler (1965) and Ziegler et al. (1968).

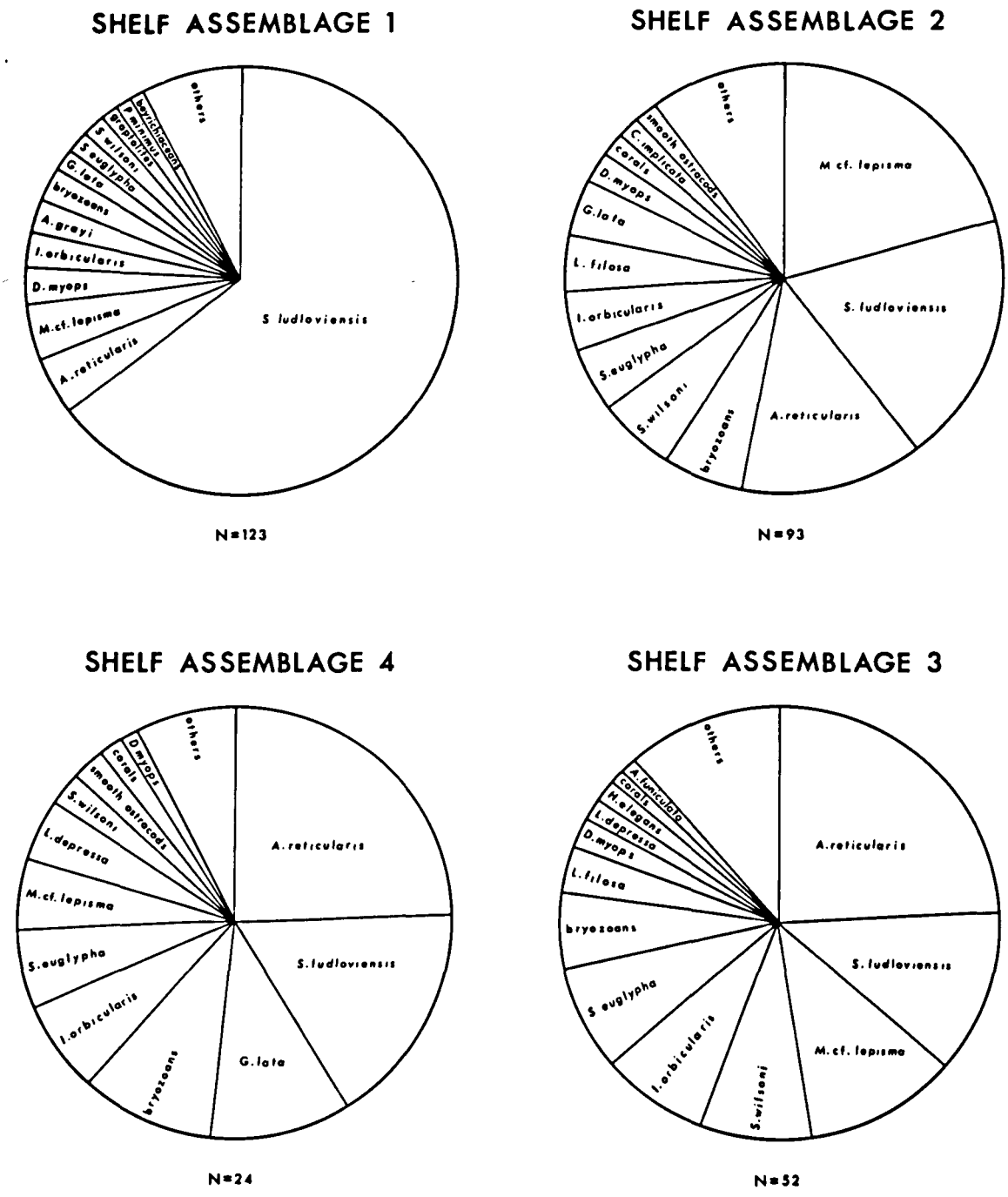

Fig. 3·15 Commonest organisms in each Lower Bringewoodian shelf assemblage. N = Number of samples used in compiling each diagram.

Like these latter authors Calef & Hancock considered their 'communities' were associations of species which responded similarly to the physical environment in which depth was the controlling factor. Sediment type was not thought to be a controlling factor; Calef & Hancock (1974, p.797) claimed that there was no correlation between sediment type and 'community'. Similar views were expressed by Ziegler et al. (1968). Instead Calef & Hancock (1974, p.803) considered that an alleged decrease of food with increased depth was the factor controlling brachiopod distribution.

Hancock et al. (1974) considered that the deepest water Ludlovian 'community' (Visbyella) possibly lived in depths of water up to 1500 m. This value was derived by comparing changes in brachiopod size, diversity, density and 'biomass' in Silurian communities with modern examples in a transect from shallow to deep water. Shabica & Boucot (1976), however, argued that the comparison of 'biomass' between Silurian and modern communities, quoted by Hancock et al. (1974) to determine the depths to which the former ventured, was invalid because: a) the former were dominantly epifaunal suspension feeders, while the latter are dominantly infaunal deposit feeders so both groups would respond differently to the same environmental factors, b) depth did not control all environmental factors, c) the assumption by Hancock et al. (1974) that animals were spheres for calculating volume and hence 'biomass' changes produced erroneously large values and hence misleadingly suggested very deep water, d) the diversities of Hancock et al. (1974) were calculated in a different way to the modern work they quoted and therefore the two are not comparable and e) the absence of imploded cephalopods in the 'Visbyella community' suggests that this 'community' lived well above 600 m. From a consideration of all these factors Shabica & Boucot (1976) suggested that the 'Visbyella community' had a maximum depth range of 200 m.

Cherns (1977, 1979) noted that 3 of Calef & Hancock's 'communities' alternated in less than 1 m of Lower Leintwardinian strata. Since it was not possible to envisage depth changes of many tens of metres at a minimum (Shabica & Boucot 1976) or hundreds of metres at a maximum (Hancock et al. 1974) occurring over such short distances it appears that Calef & Hancock's 'communities' are not indicative of depth.

Lawson (1975) severely criticised the methods by which Calef & Hancock (1974) sampled to establish their 'communities'. He further noted (op. cit., p.521) that some potential controlling environmental factors on faunal distribution such as substrate, sedimentation, turbulence, salinity and food may vary with depth but are not directly controlled by

it, e.g. muddy substrates and still waters are commonest at great depths but are not uncommon in shallow water and therefore caution is needed. Lawson (1975, p.522) also noted that it had long been recognised by Ludlovian workers that faunal assemblages varied with facies, contrary to the claim by Calef & Hancock (1974, p.797) that no correlation between the two existed. Lawson (1975) concluded that the emphasis on depth communities had led to the neglect of other factors affecting faunal distribution, such as substrate.

Indeed Watkins (1975, 1979) in a more thorough study of Ludlovian benthic 'communities' than Calef & Hancock found that lithological facies and 'community' changed together and therefore concluded that the physical environment was the major influence on faunal distribution, with changes in bottom type, sedimentation patterns and hydrographic conditions exerting influences on the fauna.

Watkins (1975, 1979) also argued that similar environments and therefore similar faunas can exist at different water depths. He reviewed work on present day faunas and concluded that modern 'communities' are influenced by many different environmental factors. Where such environmental factors parallel bathymetry then sedimentary facies zones are orientated parallel to the coastline and therefore 'communities' occur in depth related bands. However, where environmental zones do not parallel the coastline, or bathymetric contours then benthic communities show a similar lack of depth relation.

Evidence to support Watkins's conclusions is also available in the fossil record. For example, Bridges (1975) has shown that the upper Llandovery palaeogeography was more complex, including a large peninsula on the site of the Long Mynd, than Ziegler (1965) or Ziegler et al. (1968) realised. The protective effects of this peninsula provided a restricted marine embayment to the east, in which the '*Lingula* community' occurs; to the west of the peninsula *Pentamerus* and *Stricklandia* 'communities' lived in open marine sands. However, Bridges data does not suggest any difference in water depth between these communities. Later in the upper Llandovery Bridges showed that the shelf possessed a fairly even bathymetric gradient with both sediments and Ziegler's communities occurring as parallel zones away from the shoreline. A further example comes from the Silurian-Devonian Keyser Limestone of the Appalachians, from which Makurath (1977) identified a variety of environments. He noted that each environment contained a fauna which was distinct from other environments and concluded that faunal distribution was related to

the distribution of depositional environments but not to either water depth or distance from shore.

From these observations we can conclude that when depositional environments parallel bathymetric contours then faunal assemblages will show a depth relationship, but when depositional environments are not parallel to bathymetric contours then faunal assemblages will not be depth related. Another major conclusion is that it is vital to establish environmental conditions, independent of faunal data.

Lawson (1975) suggested that the most promising approach for the examination of Ludlovian faunal distributions was to examine the possible functional significance of the morphological characters of each species and attempt to relate them to particular facies preferences of individual species. Such an approach was adopted for the present study.

An attempt at this kind of study, but limited only to brachiopods, was also undertaken by Fürsich & Hurst (1974) who attempted to relate lophophore size to environmental distribution in terms of water depth. Fürsich & Hurst (1974) reviewed the lophophore complexity of different brachiopod orders and concluded that in order of increasing filtering capacity (and therefore lophophore complexity) they were orthids and strophomenids, then rhynchonellids and then spiriferids and pentamerids. They argued that since less food exists in deeper water, a fact disputed by Hallam (1965) and Rhoads (1975) who considered that food was not a limiting factor in epeiric seas, brachiopods living in this environment will require a greater filtering capacity. If this is so then orthids and strophomenids would have lived in the shallowest water, rhynchonellids at intermediate depths and spiriferids and pentamerids in the deepest water. In fact Fürsich & Hurst found rhynchonellids in the shallowest water sediments. To explain this they argued that rhynchonellids were better adapted for shallow water turbulent environments. However, if the distribution of brachiopods is so strongly controlled by their efficiency of filter feeding as Fürsich & Hurst suggest, why did the strophomenids not develop adaptations to the shallow water environments their lophophores were supposedly so well adapted to (Fürsich & Hurst 1974, p.892)?

Fürsich & Hurst (1974) claim that the development of a strong fold and sulcus in spiriferids and pentamerids is an adaptation for filter feeding in quiet, deep water environments, yet rhynchonellids commonly show a strong fold and sulcus and they occur in the shallowest water of all. Fürsich & Hurst (1974) claim that Atrypa and Gypidula because of

their complex lophophores inhabited deep, quiet water environments. However, detailed work by Worsley & Broadhurst (1975) and Anderson & Makurath (1973) on these two genera respectively have shown that they thrived in moderately turbulent environments and that in the case of Atrypa quiet water environments led to stunting of the shell (p.12, 76) yet Fursich & Hurst claim it is in this latter environment that the species should thrive because of its large complex lophophore. Further exceptions to spiriferids and pentamerids living in quiet, deep water, to which Fursich & Hurst claim they are well adapted are the pentamerid Kirkidium which lived in a very shallow and turbulent water environment, possibly in the breaker zone (Newall 1966) and the spiriferid Howellella which is commonest in one of the shallowest water environments of the Ludlow, that of the Upper Whitecliffe Beds. The shells of both these species are well adapted to such turbulent, shallow water conditions (p.20, 21).

It is not therefore possible to explain the distribution of brachiopods in terms of just one factor (e.g. filtering capacity) with other adaptations modifying the distribution only slightly (Fursich & Hurst 1974, p.898); it is necessary to consider all morphological adaptations. When this is done it appears that taxa from all orders of brachiopods could live in almost any environment (suitable for brachiopods) by adapting their shells. This is in fact shown by Fursich & Hurst (1974, Fig. 6) where on basic morphological features it is shown that all orders of brachiopods (except strophomenids), can develop the necessary adaptations to live in both turbulent (shallow?) and quiet (deep?) water environments. The filtering capacity of the lophophore does not appear to affect this distribution. This fact was confirmed by Cooper (1972) who looked at homeomorphy in brachiopods from the abyssal depths off California. The only three brachiopods occurring there were a rhynchonellid and two terebratullids, which should according to Fursich & Hurst (1974) live at very different depths, since their filtering capacities are very different, yet they are all obviously well adapted to this quiet water environment, they are all thin shelled, smooth, sulcate and globose and are very similar. Again it appears that morphological adaptations of the shell are far more important than filtering capacity of the lophophore in controlling the distribution of these forms.

It is therefore necessary to examine basic morphological features which, it is argued, will give far more information about the environment

the animal was adapted to than the inferred filtering capacity of the lophophore.

In this study all the morphological adaptations of each taxon, as well as all physical environmental parameters deduced from a study of the sediments, were considered before the most important and controlling factors of both were decided upon. From such an approach it was shown possible to explain the observed distribution of each Lower Bringewoodian shelf taxon. A similar approach is now adopted to explain the distribution of the faunal assemblages in the shelf strata examined during this study, as outlined in the previous section.

During the Upper Eltonian very low energy, quiet water, distal conditions prevailed over the whole shelf, with fine material settling out of suspension. Bioturbation is rare, suggesting that bottom waters were not fully oxygenated due to poor water mixing. Increased bioturbation at Usk and Brookend suggests greater water mixing and therefore better oxygenation in these areas. The low diversity, low density fauna of mainly pelagic graptolites, nektic orthocones and S. ludloviensis clearly reflects the unfavourable bottom conditions for benthos. The small size of the benthic fauna is very marked. However, this small size would make them ideally adapted to low oxygen levels (Raff & Raff 1970) and since poor oxygenation implies lack of currents which would supply nutrients and because small animals require less food per individual, a population of them will stand a better chance of survival in these conditions. The increase in benthic forms in the more south-easterly exposures reflects the increased water mixing and therefore better oxygenation in these areas.

The change from the Upper Elton Beds to the Lower Bringewood Beds is marked by an abrupt change in fauna and facies with very little transition. The most likely cause is thought to be an increase in turbulence across the whole shelf at the base of the Lower Bringewoodian. The extensive and complete bioturbation of shelf sediments, the increase in diversity and density of the fauna, especially the benthos, the presence of storm deposits and the appearance of bryozoans and corals reflect these environmental changes; the improved water circulation appears an especially important factor. The bioturbated siltstone facies is the dominant lithology of the Lower Bringewood Beds in all sections. An environmental gradient is deduced between a very quiet water distal shelf edge environment and a more turbulent proximal shelf environment during the deposition of this facies. Paralleling this environmental

gradient there is a gradual change in emphasis of the fauna across the shelf. It is possible to divide the fauna of this facies into 3 associations (p. 88), although this is totally artificial since they completely intergrade forming a faunal continuum across the shelf (Figs. 3.12, 3.14). The 'outer shelf' assemblage is dominated by small, smooth, thin shelled, unattached brachiopods (e.g. S. ludloviensis) which are well adapted to the quiet water conditions with possibly below normal oxygen and food levels which are considered to have existed. The 'middle shelf' assemblage is marked by a decrease in the abundance of forms such as S. ludloviensis and an increase in larger, thicker shelled, although still largely smooth and unattached forms adapted to the slightly, but significantly, more turbulent environment which apparently existed. The 'inner shelf' faunal assemblage is dominated by large, thick shelled, strongly ribbed brachiopods, many of which were pedically attached, these are ideally adapted for the moderately turbulent conditions which apparently existed; unattached, free forms such as M. cf. lepisma, were not and are consequently rarer.

The nodular bioturbated siltstone facies of the Lower Bringewoodian occurs as a sudden change in lithology and are considered to represent sudden, relatively short lived, increases in turbulence (as seen in the Upper Bringewoodian (Newall 1966)). These strata represent the highest energy environment discussed so far and the fauna reflects this with a dominance of strong, large, thick shelled, mostly heavily ribbed brachiopods. The common occurrence of bryozoans and corals reflects the good water circulation and lack of turbidity. The four Lower Bringewoodian shelf assemblages are illustrated in Fig. 3.15.

During the deposition of the Lower Bringewoodian storms periodically swept across the shelf throwing sediment into suspension and scouring the fauna from the sea bed and depositing it as shell beds in storm deposits. A low degree of scour is indicated by the virtual absence of infaunal species from these deposits. The abundance of various taxa in these deposits can be markedly different from the surrounding sediments reflecting the degree of transport they have undergone. Storm deposits are commoner and thicker in the more proximal 'inner shelf' areas and thinner and rarer in the 'outer shelf' areas where they appear to have transported the fauna and sediment less, indicating a more distal environment, near to the limit of storm influence.

The sudden facies change at the base of the Upper Bringewoodian indicates a further shelf wide increase in turbulence with a high, but variable energy environment now existing over the whole shelf and deposition everywhere apparently above wave base. In these clear,

shallow, well circulated waters corals thrived, at times forming 'reef' masses at the shelf edge barrier. Brachiopods, however, still dominate most of these beds, almost all are large, thick shelled, strongly ribbed form, well adapted to such high energy conditions.

The changes in diversity seen in the faunal assemblages can be explained by the existence of greater physiological stress in some environments reducing diversity (e.g. Sanders 1968, 1969; Slobodkin & Sanders 1969; Sanders & Hessler 1969). The explanation for the high diversity in the Lower Bringewoodian relative to the Upper Eltonian and Upper Bringewoodian can therefore be explained in terms of the relatively high stress conditions in the Upper Eltonian created by poor water circulation and below normal oxygenation and in the Upper Bringewoodian from strong turbulence and a high (but fluctuating) energy environment. Within the Lower Bringewoodian the higher diversities of the 'middle shelf' assemblages, compared to those of the 'inner' and 'outer shelf', can be explained, since greater directed stress on organisms existed in the outer shelf from poorer water circulation and therefore possibly not fully oxygenated waters and a low nutrient supply, and in the inner shelf from more frequent destruction of the fauna by storms and a higher energy, more turbulent, environment. Workers on modern faunas have also found that diversity changes along a stress gradient, with the highest diversities existing in the lowest stress environments (e.g. Sanders 1968; Sanders & Hessler 1969; Johnson 1970, 1971; Rhoads & Morse 1971; Stanton & Evans 1972).

The degree of physiological stress is also thought to have controlled faunal density. Therefore the lowest diversities exist in: a) the unfavourable poorly circulated and possibly not fully oxygenated environment of the Upper Eltonian, b) the possibly not fully circulated and subnormally oxygenated environment of the 'outer shelf' Lower Bringewoodian and c) the turbulent, high energy environment of the Upper Bringewoodian. The highest faunal densities are noted in the most favourable less stressful environments of the 'middle' and 'inner shelf' of the Lower Bringewoodian. Calef & Hancock (1974, p.803) have proposed that an alleged decrease in food supply with increasing depth was responsible for decreasing faunal density in increasingly deeper water environments. However, the decrease of faunal density from the Lower Bringewoodian into the shallower water environment of the Upper Bringewoodian shows that this model of food supply controlling faunal density is erroneous. Furthermore, food was probably not a limiting factor in epeiric seas

anyway (Hallam 1965; Rhoads 1975) excepting conditions of poor water circulation.

Johnson has argued that the reason fossil 'communities' are continuous or discontinuous is dependent on the slope of the environmental gradient; if the environment is gradational then the 'communities' will be gradational but if there are sharp breaks in the environmental gradients then 'communities' will appear discontinuous. Work on modern faunas has also indicated that faunal gradients correlate with environmental gradients (e.g. Sanders & Hessler 1969; Johnson 1970, 1971; Rhoads & Morse 1971; Dörjes 1972; Jackson 1972) and that a whole complex of environmental factors controls the faunal distribution. Therefore during the period of Ludlovian history examined in the present study there appear to have been extensive periods during which the environment was fairly constant; between these periods rapid and marked environmental changes took place (e.g. at the base of the Lower Bringewoodian). However, within each 'overall' environment conditions were not entirely uniform and environmental gradients existed within them (e.g. the proximal-distal gradient in the bioturbated siltstone facies). The close correlation of fauna and facies suggests a strong control of the former by the physical environment.

Throughout this chapter terms such as high energy, low energy, very turbulent etc. have been used to describe environmental conditions. This is not to suggest that the dynamic state of the water was the only factor affecting the fauna at this time, however, they are useful descriptive terms and also indicate the degree of other important environmental influences such as turbidity and the extent to which bottom waters were aerated. It is, however, interesting to note that Stanley (1970, p.12, 13) considered that the most important environmental factor influencing bivalve distribution was water movement because of its influence on other major physical environmental parameters such as substrate character, degree of sedimentation and food. In fact Hallam (1965, p.138) considered that the importance of sediment type is the indication it gives of water movement strength and it is the latter which is the more fundamental factor affecting faunal distribution. Schmidt is also quoted by Shafer (1972, p.472) as recognising that the degree of water agitation is the paramount influence on both sediment character and faunal distribution.

Conclusions

A detailed examination of the faunal distribution, environmental interpretations from sedimentological studies and a review of the functional morphology of individual taxa suggests that a whole complex of physical environmental factors (e.g. variations in turbulence, turbidity, oxygenation and nutrition levels of bottom waters, sedimentation rate, sediment characteristics etc.) were responsible for controlling the distribution of fauna at this period in Ludlovian history.

Physical environmental changes influenced the quantitative and qualitative characteristics of faunal assemblages. As certain conditions became limiting for individual species they became rare or even stunted, while others better adapted to the new environment entered the fauna or markedly increased in abundance; species occur together where their environmental tolerances overlap. There appears to have been a large degree of species independence, however, predators (e.g. orthocones and some trilobites) must have been limited by the distribution of their prey and ostracods may have been strongly influenced by algal types.

Although Calef & Hancock (1974) and Fürsich & Hurst (1974) have suggested that variable food supply with depth was the most important single factor in controlling the distribution of brachiopods, and presumably other taxa, the evidence presented above suggests this is not so.

CHAPTER 4

THE BASIN-SECTIONS, SEDIMENTOLOGY AND FAUNAS

SETTING

Shape

Mapping of the thick Ludlovian basinal succession to the west of Aymestrey and Leintwardine has been carried out by Stamp (1918, Bucknell), Straw (1937, Builth Wells and 1953, Cwm Graig Ddû), Earp (1938, Kerry and 1940, South-West Clun), Kirk (1948, 1951, Brecon 'Anticlinal') and Holland (1959, Knighton). Each of these workers used local classifications, dividing the rocks into stratigraphical units using both faunal and lithological criteria. These local classifications have since been correlated by Holland *et al.* (1963) and Cocks *et al.* (1971), see Fig. 1.4, mainly on graptolite evidence, as the shelly, benthic, fossil assemblages differ at the same level in different areas.

Some of this earlier work also began to create a palaeogeographical picture. The 'contorted beds' found within the successions at various localities were interpreted by Straw (1937) and Earp (1938, 1940) as the results of mass sliding of soft sediment, under gravity, down submarine slopes at various intervals during deposition. Sedimentological work on the Ludlovian basinal sediments by Cummins (1959a, 1959b) established the shape of the basin as a narrow trough (the Montgomery Trough) bounded by palaeoslopes to the west and east down which he assumed sediment slumped inwards towards the trough axis; down this axis turbidite currents flowed towards the north. The west slope of the basin flanked the Derwen Ridge which separated the Montgomery Trough from the Denbigh Trough in North Wales.

The existence of a boundary slope into the basin in the east and south-east was suggested by Holland & Lawson (1963) from isopach maps and a facies change from shelf to basin. These indicate a north-east to south-west striking slope which swings north-south towards the north and approximately follows the Church Stretton Fault complex (Ziegler 1970; Bailey 1964, 1969; R. Marsh 1976; Bailey & Woodcock 1976) see Figs. 1.1 and 4.1. Williams & Prentice (1958) investigated slump folds and crinkle marks in the *incipiens* (*tumescens*) Zone of the area around Ludlow and concluded that they both indicated sediment movement down a north-west facing slope. At Builth Wells and Cwm Graig Ddû, Straw (1937, p.447; 1953, p.212) noted slump evidence which suggests a north-west facing slope in this region.

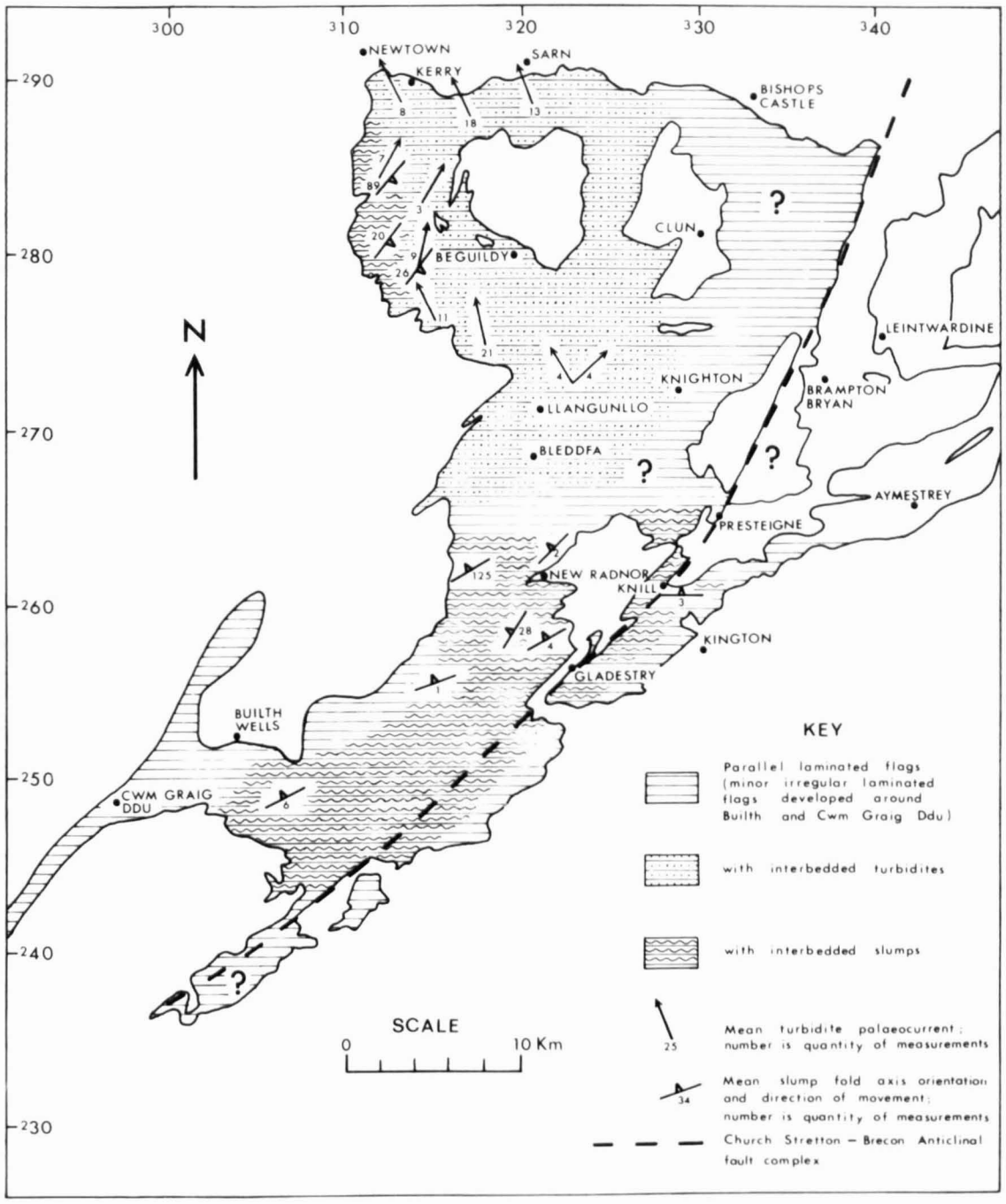

Fig. 4.1 lower Bringewoodian basinal sedimentation patterns. Includes work by Kirk (1948) , Bailey (1969) and Woodcock (1976b) which incorporates data from upper Eltonian and upper Bringewoodian sediments too. Slump data from Knill and Builth, and turbidite data from Kerry from present work.

The boundary slope to the west of the basin, suggested by Cummins (1959b), was considered by Bailey (1964, 1969) from slump fold axis measurements to strike north-east to south-west; he argued that since the slump sheets of this region are known to have spread south-east with time (Earp 1938) into the area of turbidite deposition in the axial region of the trough then, if the slope down which the sediments slumped faced north-west, the spread in slumping to the south-east would have involved turbidite beds which had been deposited earlier. This is not so; slumping therefore must have been from a south-east facing slope, beyond the limit of turbidite deposition.

Woodcock (1974, 1976a) established that the slump sheets of the Ludlow Series in Wales were not teconic folds. By detailed measurement and study of many slump folds Woodcock (1976b) concluded that on the eastern margin of the basin the slope hada mean north-east to south-west strike and faced the north-west. While on the western margin the slope, although also trending north-east to south-west, dipped to the south-east; thus confirming the model established by Cummins (1959b, 1969) and Bailey (1964, 1969) of a narrow trough down whose axis north flowing turbidite currents moved and on whose bounding slopes sediment slumped towards the axial region. Bailey (1964, 1969) and Cummins (1969) took the turbidite belt as evidence for an essentially flat basin floor with a gentle dip north, inducing turbidite flow along the axis. This floor was probably up to 15 km wide and flanked by marginal slopes. The facies distribution in such a trough would show an abrupt transition from turbidite to slope facies at the slope-floor break; slumping would only affect slope sediments, since from mathematical models no individual slump could advance far over a flat trough floor (Woodcock 1976b). The slump sheets would therefore accumulate in the region of the slope-floor break forming a rise at the base of the slope (Woodcock 1976b). However, when the facies distribution was examined, interdigitation of the slump and turbidite facies was found for lateral distances of 2 to 5 km; since slumps could not have advanced this far over the flat trough floor Woodcock (1976b) explained this feature by turbidite currents depositing sediment on slump rises rather than emplacement of slump sheets on a level trough floor as Bailey (1967, 1969) had argued. The presence of slumps therefore indicates a position on the palaeoslope.

Nature Of The Bounding Palaeoslopes

As noted before, the line of the shelf-basin transition approximately follows the Church Stretton Fault complex so that the rapidly

subsiding basinal area lay to the west and the contemporaneous shallow 'shelf sea' to the east. Holland & Lawson (1963) have correctly noted that basinal sediments occur to the east of the fault (e.g. the Knill section examined in this study lies 1 km to the east of the fault but has a basinal facies and fauna); however, these sediments contain slumps and therefore lay on the palaeoslope (Woodcock 1976b), so that this eastern palaeoslope lay across the present fault line.

The sharp transition from shelf to basin facies, involving a rapid increase in the thickness of deposits over a zone only a few kilometres wide (Figs. 1.2, 1.3), through which a major basement fracture runs implies that a fault controlled eastern margin to the basin existed. This fault control apparently operated previously, since Greig et al. (1968, p.75, 104) argued that the Church Stretton Fault complex influenced sedimentation in the Longmyndian and Caradocian. Bailey (1969) and Ziegler (1970) have argued that the eastern margin of the Ludlovian basin was maintained by relatively greater subsidence of the basement to the west of the fault. It appears therefore that the fault was active during Ludlovian times and deposition of silt and mud on this unstable fault controlled palaeoslope probably produced slumping and turbidite currents (Bailey 1969).

A fault control for the eastern boundary therefore seems likely but it is not possible to observe the western boundary of the basin as it is unexposed. However Ziegler (1970) has argued it too was fault controlled so that the greater subsidence of the basinal region, relative to the surrounding area, was due to block faulting of the basement rather than crustal downwarp. Ziegler (1970) suggests that the apparent horst and graben structure of the Welsh Borderland is not unlike basins off south California today. Dewey (1969, p.125) also considered that the Welsh Basin was a fault controlled (intracratonic) basin.

Water Depth In The Basin

The depth of water in the basin must have been greater than that on the shelf since sediments deposited in the former include numerous slump and turbidite horizons containing faunal assemblages derived from the shelf and unknown from indigenous basinal sediments. However, the actual depth of water is difficult to deduce.

Cummins (1969 quoting Kuenen 1964) noted that there appears to be a connection between modern turbidites and abyssal plains. He therefore assumed that all areas of the Silurian sea floor where turbidite deposition was taking place were at abyssal depth. Cummins (1969)

however does note that if Holland & Lawson's (1963) claim that the basin turbidite facies was closely bounded to the east by shelly limestones and silt in Bringewoodian times, then the depth of water in the basin, at this time, may have been only about 90 m (300 feet). However, Bailey (1964) found turbidites extending no further east than Bishops Castle, some 11.5 km to the west of the boundary given by Holland & Lawson and on this evidence Cummins (1969) considered there might still have been an appreciable depth difference between the area of turbidite deposition and the shelf.

Bailey (1969) regarded the finely flaggy siltstone lithology which he described as occurring in the basinal Bringewoodian, both alone and interbedded with turbidites or slumps, as indicating deposition at bathyal depth because the great regularity of the bedding and lamination suggests that it accumulated beyond the range of wave and tidal currents.

It therefore appears that water depth in the basin during the Bringewoodian was quite substantial and certainly considerably greater than over the adjacent shelf area.

RECOGNITION OF THE LOWER BRINGEWOOD BEDS IN THE BASIN

Correlation of the basinal strata with those of the shelf, including the type area, has always been difficult since the lithology and fauna are so different and because at this level the graptolites of the basin are usually poorly preserved long ranging forms. However, as shown in the following discussion of the basinal sections examined in this study, it is possible to recognise the approximate position of lower Bringewoodian deposits in the basinal succession.

The local stratigraphic units established by basinal workers have been correlated with the type succession at Ludlow by Holland *et al.* (1963) and Cocks *et al.* (1971) using graptolites. The local basinal divisions correlated with the Lower Bringewood Beds were examined in the field in an attempt to confirm these correlations. If the local units were large and spanned several divisions of the Ludlow, then they were arbitarily subdivided by the number of Ludlow divisions they have been correlated with, assuming the rather unlikely factor that each division is represented by the same thickness in the basinal succession. When these beds were examined in the field attempts to find graptolites which would position the lower Bringewoodian more accurately were made. If no such graptolites were found then the above correlations were considered to be as accurate as possible given the data available. When identifiable

graptolites were found they were either long ranging species or at best, they only indicated the incipiens Zone, which spans 3 divisions of the Ludlow i.e. Upper Eltonian to Upper Bringewoodian (Holland et al. 1963; Cocks et al. 1971) and so the strata identified as belonging to this zone could not be subdivided by any means other than assuming that equal thicknesses represent each Ludlow division with the middle third corresponding to the lower Bringewoodian.

Although this is obviously a very crude approach, the lack of any alternative meant that it was the only one which could be adopted here. However, even if some of these correlations are slightly erroneous, it is not as unfortunate as it may seem because throughout the incipiens Zone, and beyond in some cases, many basinal sections show a constant lithology, indigenous fauna and therefore presumably represent a stable environment; so even if the direct equivalents of the shelf Lower Bringewood Beds were not being examined the palaeoecological and sedimentological information collected from the strata examined are still valid for them.

BASIN SECTIONS

Each of the sections through the basinal lower Bringewoodian examined during this study is considered in turn; again charts are presented to accurately and quantitatively indicate the abundance of each taxon, the lithological variation up each section, the position of samples collected and the density and diversity of each sample. From these charts (Figs. 4.2 to 4.6) faunal variation can be examined in a quantitative way. A key to symbols used in these charts is given in Fig. 3.1. As each section is considered its geographic location, position of samples from it and the criteria used for recognising the lower Bringewoodian are discussed.

i) Knill

The area around Knill forms part of the region mapped by Kirk (1948, 1951) who included all the beds in the incipiens (tumescens) and leintwardinensis Zones (i.e. the Upper Eltonian to Lower Leintwardinian (Holland et al. 1963; Cocks et al. 1971)) in a division she termed the Striped Flags. The section examined here is in a forestry road cutting about 0.5 km south of Knill Church. The road appears to have been cut only recently and was certainly absent when Kirk visited the area. The section examined occurs in the south bank of a road which runs east at about 080° from SO 28755983, exposure commences at SO 29005985 and is continuous (apart from a few metres which are unexposed just beyond

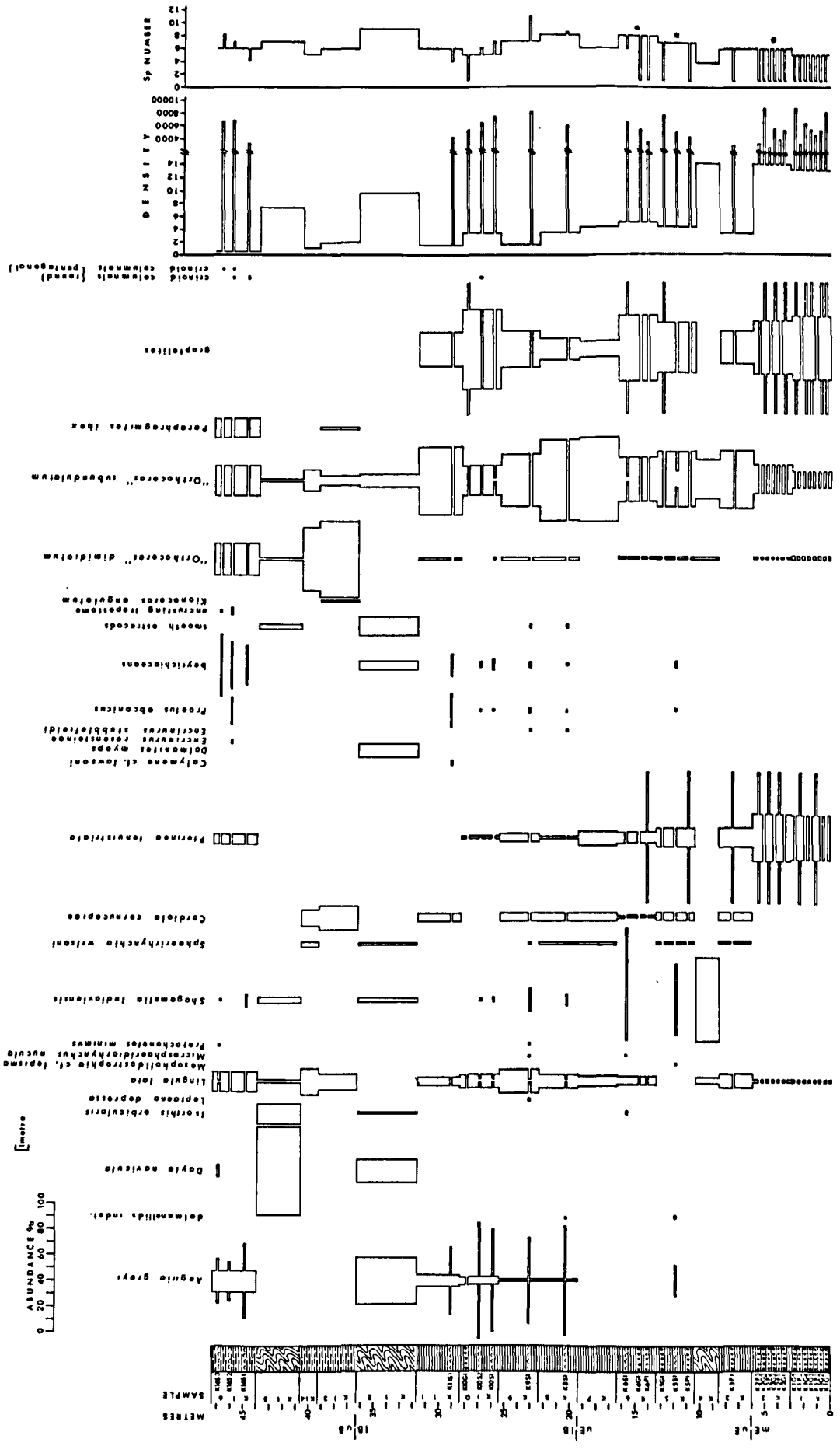

Fig. 4.2 The lower Bringewoodian succession and fauna at Knill

SO 29225992) up to SO 29726000 where Upper Leintwardine Beds (the 'C. grayi Beds' of Kirk) are exposed.

During a reconnaissance of this section abundant S. leintwardinensis graptolites were found in the beds immediately beyond the above mentioned small break in the section at SO 29225992; these indicate a leintwardinensis Zone age and therefore the underlying strata between SO 29005985 and SO 29225992 were collected to ascertain if lower Bringewoodian strata were present. Results of this investigation are summarised in Fig. 4.2.

Graptolites were absent from slumps in this section (collections K4, K12 and K15) and from the collections K13, K14 and K16. However, in all the other samples they make up a substantial part of the fauna. The abundance of S. incipiens in the graptolite assemblages of collections K3 to K11 (excluding the slump, K4) suggests an incipiens Zone age for them (Rickards 1976, p.171). The only other taxa are rare S.c. semispinosus and a new subspecies of S. varians (the latter has an unknown range). Holland et al. (1963) and Cocks et al. (1971) considered that the incipiens Zone included the Upper Elton Beds, and the Lower and Upper Bringewood Beds. However graptolites from collection K2 contain only rare specimens of S. incipiens and are mainly of S.c. semispinosus and graptolites from collection K1 are only of this latter subspecies. Collections K1 and K2 are therefore assigned to the scanicus Zone and are probably equivalent to the Middle Elton Beds (Holland et al. 1963; Cocks et al. 1971).

From the above arguments therefore the Upper Eltonian and all the Bringewoodian must lie between collections K3 and K16. It is difficult to divide up the succession between K3 and K16 into these 3 divisions with any certainty. However, collections between K13 and K16 (excluding a slump, K15) consist of irregular laminated flags with trace fossils evident on bedding planes and some (rare) beds showing complete bioturbation; rare ripple cross lamination is also present in these beds. These features are absent from the strata below and it is suggested later that such structures are the result of increased current activity. Since the Upper Bringewoodian strata of the shelf show signs of increased current activity when compared with Lower Bringewoodian lithologies, collections K13 to K16 may be upper Bringewoodian in age. If this is so (and it is impossible to be certain) then collections K3 to K12 must represent the upper Eltonian and lower Bringewoodian. The fauna and lithology of the strata between these two collections is almost identical and therefore (after deducting the thickness of slumps, since they

involved the almost instantaneous deposition of large amounts of sediment, and assuming a constant sedimentation rate and an equal time period for the deposition of both divisions) the remaining thickness of strata was divided in half so that collections K8 to K11 were assigned to the lower Bringewoodian (together with slump K12) and collections K3 to K7 (including slump K4) were assigned to the upper Eltonian. The possible inaccuracies of such an approach are realised but there appears to be no alternative.

The lower Bringewoodian deposits at Knill are therefore 16.77 m thick on the above argument. Despite a careful search no diastems were found in this thin sequence.

ii) Knighton

The area around Knighton was mapped by Holland (1956 , 1959). The Upper Bringewood Beds, Lower Bringewood Beds and Upper Elton Beds have been correlated by Holland et al. (1963) and Cocks et al. (1971) with the Middle and Upper Bailey Hill Beds of Holland (1956, 1959). The lower Bringewoodian should therefore occur somewhere in the middle third of the Middle and Upper Bailey Hill Beds. Unfortunately because of the structural complexity of the area in which the Bailey Hill Beds outcrop and the very low exposure in this area it is not possible to follow individual beds for any great distance or obtain an even modest sized section which is not folded or faulted too severely for a study of this kind.

After visiting a number of localities a relatively small section was found and examined in a structurally uncomplicated area, judged by this author, from the work of Holland (1956, 1959) to be at the right stratigraphical level. The results of this investigation are summarised in Fig. 4.3. The outcrops examined were two neighbouring roadside quarries about 1 km north-west of Llangunllo village. The first quarry at SO 21757205 exposed 6.32 m of strata from which samples N1, N2 and NTA to NTC were collected; the second quarry was at SO 21687205 and exposed a further 10.48 m of strata from which the remaining samples were taken. The amount of unexposed strata between the two exposures is estimated at 6 m, no evidence of faulting or folding (the exposures have dips of 046° 32°N and 047°44°N respectively) was seen or is shown on Holland's maps; therefore there is no reason to infer that the succession in this small area is complicated by deformation.

The graptolite assemblage from these beds includes B. bohemicus, S. varians, S.c. semispinosus and S. incipiens thereby indicating any

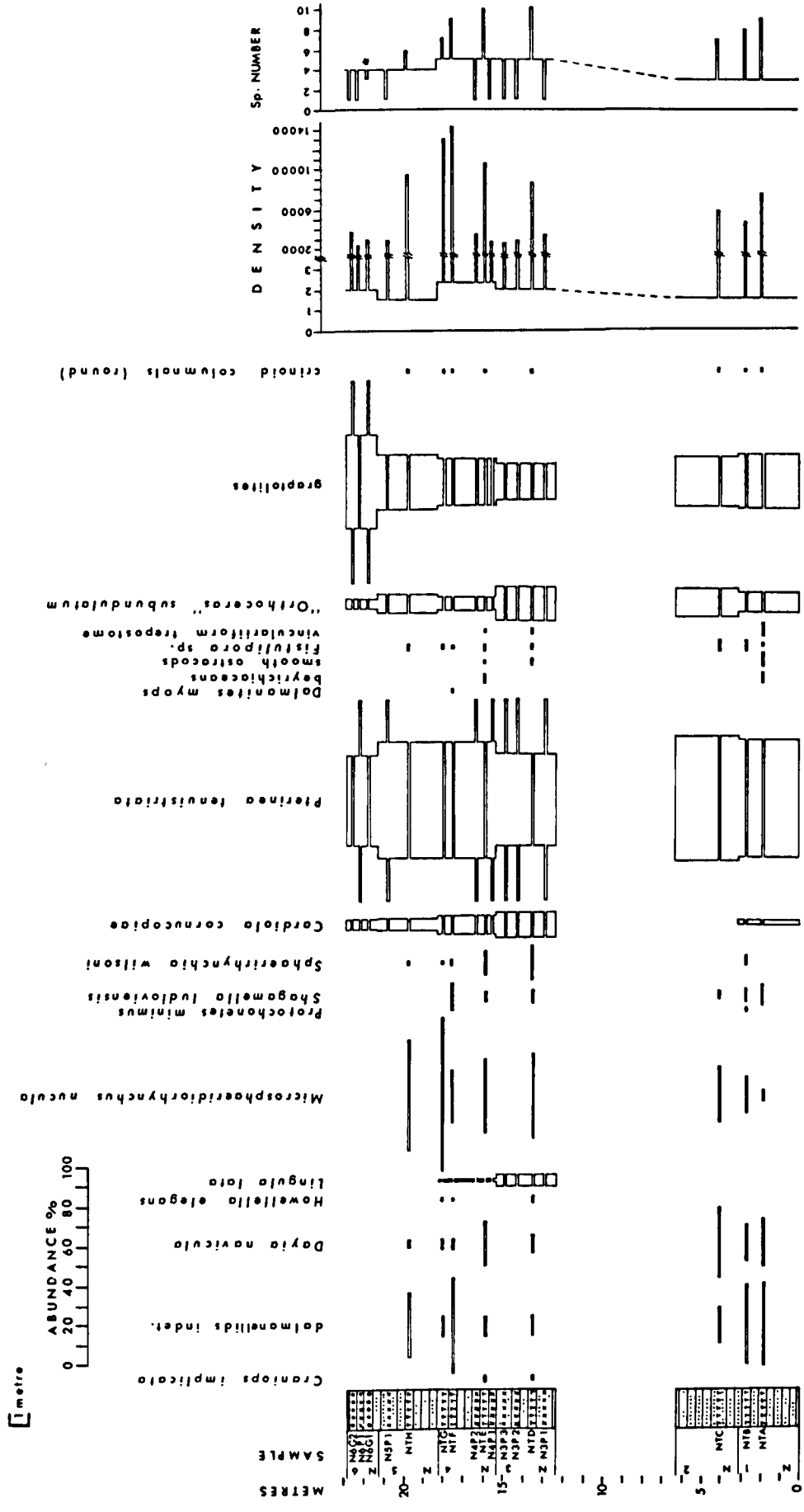

Fig. 4.3 The lower Bringewoodian succession and fauna at Knighton

horizon from upper nilssoni to lower incipiens Zone (Richards 1976, pers. comm. 1978); therefore these beds may be middle Eltonian to lower Bringewoodian in age (Cocks et al. 1971). However, although the exact position in this succession is not known this is not as big a problem as it seems. Holland (1959, p.451) noted that the Bailey Hill Beds are remarkably uniform in lithology throughout, a fact confirmed during the reconnaissance of the Knighton area undertaken in this study. Although Holland (1959, p.452) refers to broad faunal changes through the thickness of the Bailey Hill Beds, during this study the taxa he quoted as 'varying' were all found to occur only in the bases of turbidites. The taxa found in turbidite soles are largely benthic fossils which have been swept from the shelf by turbidite currents into the basinal sediments in which none of them are found, outside the bases of turbidites. The fauna found outside the soles of turbidites is very sparse consisting almost entirely of epiplanktic and planktic forms, bottom conditions, in the basin, appear to have been inimical to almost all benthic forms. During the reconnaissance of the Knighton area undertaken by the author, this sparse fauna was found to be identical in proportion and composition throughout what Holland (1956, 1959) regarded as Middle and Upper Bailey Hill Beds. Therefore any palaeoecological, or environmental deductions from the sedimentology, made from the detailed examination of the two quarries are valid for the lower Bringewoodian whether these strata are directly equivalent to the Lower Bringewood Beds or not since the lithology, fauna and hence environment were constant in this area during the upper Eltonian and the whole Bringewoodian.

Due to the structural complexities of the Knighton area, Holland (1956, 1959) was unable to establish the thickness of the Bailey Hill Beds in this region. He therefore used the figure of 3500 feet which Earp (1940) had deduced for equivalent but undisturbed strata in the adjacent S.W. Clun area. The Uppermost Bailey Hill Beds are noted by Holland (1959, p.458) as being 100 feet thick; these beds contain the graptolite S. leintwardinensis and are therefore clearly Leintwardinian in age. The remaining 3400 feet (1036 m) was correlated by Holland et al. (1963) and Cocks et al. (1971) with the top half of the Middle Elton Beds to the Upper Bringewood Beds i.e. 3.5 divisions of the Ludlow as defined by Holland et al. (1963). Assuming constant sedimentation and an equal period of time for the deposition of each division the lower Bringewoodian deposits may be 296 m thick in the Knighton area. The assumptions above are obviously liable to error but the figure deduced is not unreasonable

and even if it is not entirely correct it is the best that can be deduced from available information.

iii) Kerry

Earp (1938) mapped the area around Kerry. The top half of the Middle Elton Beds, the Upper Elton Beds and the whole of the Bringewoodian have together been correlated with the unit mapped by Earp as the '*Wilsonia wilsoni* Grits' (Holland *et al.* 1963). The most complete section of the '*W. wilsoni* Grits' is seen in Drefor Dingle (Earp 1938, p.131) which is about 3 km south-east of Kerry village. The section was examined during this study and the results are summarised in Fig. 4.4.

As the slope of the dingle floor and the dip of the beds were about constant over the exposure of the '*W. wilsoni* Grits' it was possible by dividing the outcrop width of this unit by 3.5 (i.e. the number of divisions of the Ludlow it has been correlated with), and assuming each Ludlow division is represented by an equal thickness of strata, to get an approximate idea of where the lower Bringewoodian should outcrop in the dingle. If the above reasoning is correct then no beds equivalent to the bottom half of the lower Bringewoodian are exposed in the dingle but much of the top half are. These strata were therefore examined in detail, they are exposed between SO 17508852 and SO 17688837. Of the 114.79 m of strata inferred to be present between these two localities only 54.79 m are actually exposed.

Graptolites are very poorly preserved in these beds but appear to be of only two species *S. clunensis* and *B. bohemicus* which indicate upper *scanicus* Zone to lower *incipiens* Zone (Rickards 1976) which range from upper Middle Eltonian to Lower Bringewoodian in age (Cocks *et al.* 1971).

Although the tentative suggestion from outcrop width that the strata examined are probably lower Bringewoodian in age is not disproved by the graptolite evidence, it does not prove that they are definitely of this age either. However, it is suggested that it is likely these beds are lower Bringewoodian on the above evidence. But even if the strata examined do not exactly correlate with the Lower Bringewood Beds the palaeoecological and sedimentological information gained from these rocks is valid since the same lithology, of laminated flags interbedded with numerous turbidites (some with fossiliferous bases), persists throughout the '*Wilsoni wilsoni* Grits'. Since the lower '*W. wilsoni* Grits' contain definite *scanicus* Zone graptolites, the '*W. wilsoni* Grits' are overlain by strata yielding *S. leintwardinensis* and diastems are lacking in this

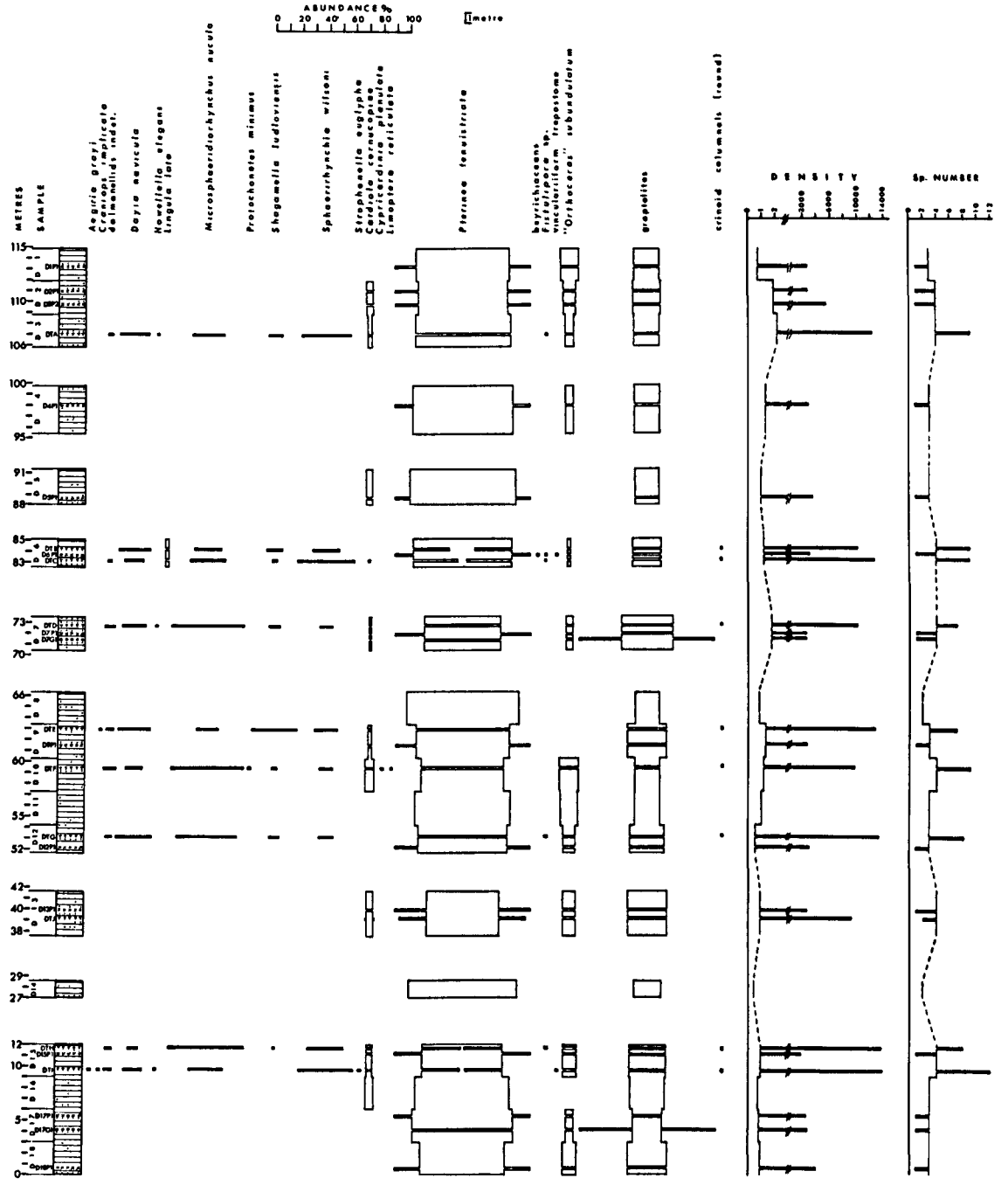

Fig. 4.4 The lower Bringewoodian succession and fauna at Kerry

succession the lower Bringewoodian must be represented in this section. The sparse very low density and diversity non benthic fauna found in the laminated flags of the succession was also found to be constant from a reconnaissance of the whole '*W. wilsoni* Grits' thickness in the dingle. The fauna found in the base of some turbidites is of mostly benthic forms (cf. the non benthic nature of the fauna in the interbedded laminated flags, which suggests an environment inimical to benthos); this fauna does vary in composition (Earp 1938) but clearly it has been transported in from shelf localities, where benthic forms thrived, and these variations reflect changing conditions in the source area for the turbidites and not in the environment in which they are now found. This latter environment is seen to be constant throughout the deposition of the '*W. wilsoni* Grits' since the lithology and indigenous fauna remain unchanged. Since this unit must include representatives of the Lower Bringewoodian, sedimentological and palaeoecological information from the strata examined in this study will be 'true' for the Lower Bringewoodian whether the strata examined correlate exactly with them or not.

Earp (1938) estimated that the '*W. wilsoni* Grits' were 2500 feet (762 m) thick; again assuming that each of the 3.5 Ludlovian divisions used for correlation is represented by an equal thickness of strata it follows that the lower Bringewoodian deposits are 218 m thick in this area. This estimate is the best that can be arrived at given the available information.

iv) Builth Wells

The area south of Builth Wells was mapped by Straw (1937). The Lower Bringewood Beds have been correlated by Holland *et al.* (1963) and Cocks *et al.* (1971) with the top two-thirds of the *Pterinea tenuistriata* Beds and the bottom two-thirds of the '*Atrypina*' Beds as mapped by Straw. The former are up to 1400 feet (427 m) and the latter are up to 150 feet (46 m) thick; therefore here, the lower Bringewoodian is up to 316 m thick (i.e. 285 + 31 m).

The beds examined during this study are on the westerly flanks of Aberedw Hill approximately 3.5 km south-east of Builth Wells. The results of this investigation are summarised in Fig. 4.5. The collections B1 to B3 were made at SO 07364941 where crags expose 7.6 m of strata. From Straw's map these are estimated to be about 180 m from the top of the *Pterinea tenuistriata* Beds. There follows what is estimated to be a 15 m gap before more crags higher up the hill expose a further 18.6 m of strata at SO 074494 from which samples B4 to B9 were collected. Further

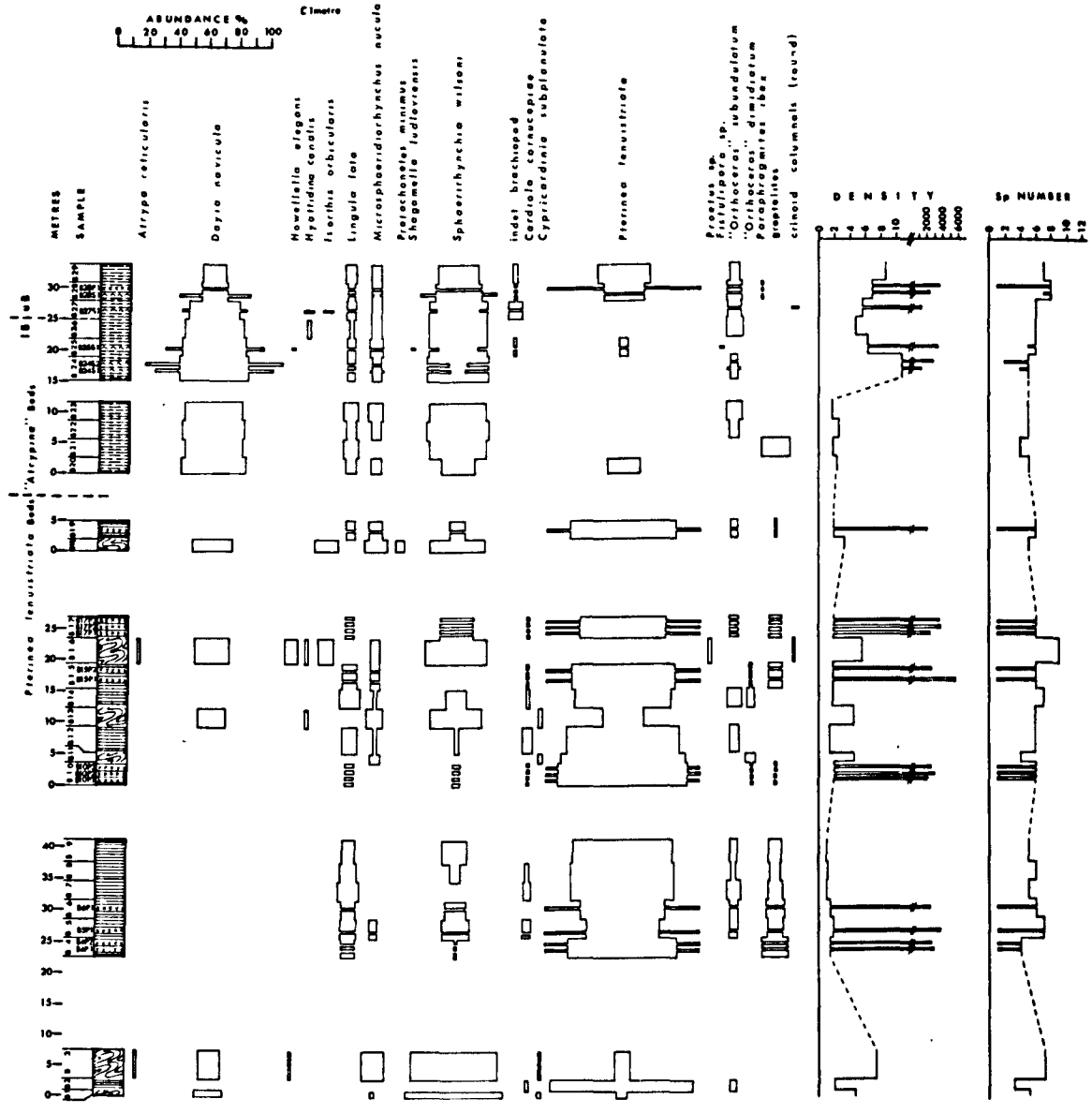

Fig. 4.5 The lower Bringewoodian succession and fauna at Builth Wells

outcrops were examined in the crags at SO 071489 where 27.23 m of beds are exposed (from which samples B10 to B17 were collected) the base of these crags, from Straw's map, is estimated to be about 140 m below the top of the P. tenuistriata Beds and therefore the gap between collections B9 and B10 is probably very small. A small extremely overgrown quarry at SO 06994854 exposes 4.85 m of strata from which samples B18 and B19 were collected. In 1937 Straw described this quarry (then exposing far more strata than at present) and the succeeding beds in the railway (now removed) embankment where the junction between the P. tenuistriata Beds and the 'Atrypina' Beds could be seen. This section is now extensively overgrown and the junction is no longer visible. However, from Straw's description and map it is estimated that the highest beds now exposed in the small quarry are about 20 m below the junction and the lowest strata ('Atrypina' Beds) exposed in the embankment are some 6 m above it.

The lowest beds in the railway embankment occur at SO 07014841 and the ascending succession can be followed south along the embankment and then into the quarries above it; the highest beds in the quarries are exposed at SO 07104818. Between these 2 localities 34.1 m of strata exist and all but 3.6 m are exposed. Samples B20 to B29 were collected from this section. Since it is estimated that this section started some 6 m into the 'Atrypina' Beds the top beds of the quarry must be some 40 m above the base of this unit which Straw (1937, p.419) estimated as 150 feet (45.7 m) thick in this section. Since the base of the upper Bringewoodian is correlated at a horizon two-thirds of the way through the 'Atrypina' Beds the junction should lie about 30 m above the base of this unit i.e. at the base of collection B27, where it was placed.

The P. tenuistriata Beds consist of laminated flags with no trace fossils or signs of current activity and an extremely sparse low density, low diversity fauna dominated by P. tenuistriata which occasionally occurs as masses of valves covering a bedding plane. Graptolites are quite common but are very poorly preserved; most appear to be of the S. chimaera group but specific identification was not possible. B. bohemicus cf. tenuis was found but its long range makes it useless for fine stratigraphic correlation. Slumps are interbedded with these strata and yield a different faunal assemblage, although it is still low in density and diversity.

The 'Atrypina' Beds are of irregularly laminated flags. The laminations have been disturbed by trace fossils and ripple cross lamination is present. Shell seams, tool marks and orientated orthocone

shells are also present. Such features suggest current activity, which is not in evidence in the underlying strata. D. navicula and S. wilsoni now dominate the fauna which is denser than that of the P. tenuistriata Beds. Not one single specimen of a definite Atrypina was found, although an indeterminate brachiopod with a shape similar to D. navicula but with several coarse costae was found rarely. Lawson (pers. comm. 1977) also reports that he has been unable to find any specimens of Atrypina in this section.

v) Cwm Graig Ddû

This valley lies approximately 8.5 km south-west of Builth Wells, the succession here was described by Straw (1953). Holland et al. (1963) correlated the Lower Bringewoodian with the top two-thirds of the Pterinea tenuistriata Beds and the bottom third of the Lower Lingula lata Beds as mapped by Straw. The former are estimated at 1050 feet (320 m) thick by Straw (1953). Straw does not give a thickness for the latter on their own but they were measured at 106 m thick by the author, from the top of the underlying P. tenuistriata Beds to the first occurrence of the graptolite S. leintwardinensis which indicates the Upper Lingula lata Beds (Straw 1937, p.413) and was found in strata directly above collection C53. Assuming the above correlation is correct then the lower Bringewoodian is here about 248 m thick (i.e. 213 + 35 m). The base of the upper Bringewoodian being 35 m above the base of the Lower Lingula lata Beds (one third of their thickness) i.e. at the base of collection C36. The succession examined during this study is shown in Fig. 4.6.

The lowest P. tenuistriata Beds examined in the succession were those in the lowest crags in the valley (on the east side) at SN 96514726. From here the ascending succession was followed by climbing up the valley side, working in a southerly direction and then, eventually, onto the west side of the valley, until at SN 96274868 S. leintwardinensis was found indicating beds of the Leintwardinian Stage and collecting was halted. Between these two grid references 184 m of strata are present of which all but 36.9 m (in four gaps) is unexposed.

The P. tenuistriata Beds are finely and parallel laminated flags with a very low density and diversity fauna dominated by P. tenuistriata which occurs occasionally as numerous valves covering bedding planes with a very high density. Slumping is absent from the upper parts of the P. tenuistriata Beds, but is present in the lower part which are probably equivalent to the upper Eltonian and were not examined during this investigation. Trace fossils are absent.

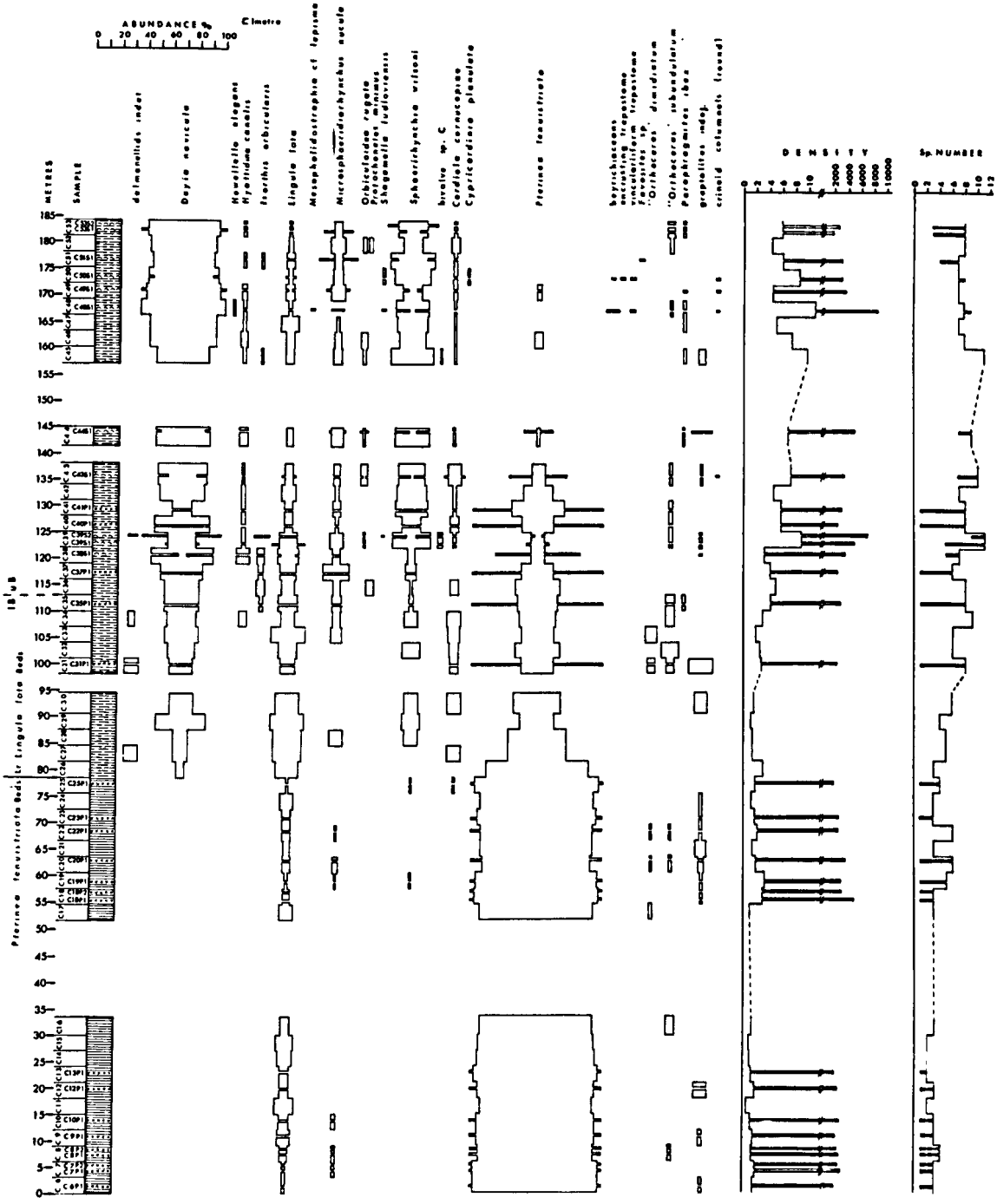

Fig. 4.6 The lower Bringewoodian succession and fauna at Cwm Craig Ddu

The Lower Lingula lata Beds are irregularly laminated flags with trace fossils, ripple cross lamination and tool marks all disrupting the lamination, which together with orientated orthocones indicate the activities of currents which were apparently absent from the underlying beds. In these beds D. navicula, S. wilsoni and M. nucula all increase in abundance as P. tenuistriata declines. However, planes of P. tenuistriata can still be found in the lower parts of these beds.

Graptolites are rare throughout the succession examined at Cwm Graig Ddû. Mostly they are too poorly preserved to be identifiable, most appear to belong to the S. chimaera group but specific identification was not possible. A few specimens of P. tumescens (indicating an upper scanicus Zone to incipiens Zone age (Rickards 1976) i.e. uppermost Middle Eltonian to Upper Bringewoodian age (Cocks et al. 1971)) were found in the lowermost beds examined.

SEDIMENTOLOGY

In order to interpret the faunal distribution seen in the basinal lower Bringewoodian sedimentological studies were carried out to deduce the environment of deposition. Detailed petrographic work was not undertaken but some 10 to 20 thin sections and over 100 polished sawn cut blocks of each lithology were examined. The different types of lithology recognised are described below.

Parallel Laminated Flags

This is the dominant lithology of the lower Bringewoodian basinal succession. It occurs interbedded with turbidites at Knighton and Kerry and with slumps at Knill and Builth Wells; at Cwm Graig Ddû it occurs uninterrupted by slumps or turbidites. (Only in the latter two localities does another lithology (irregular laminated flags) occur in the basinal lower Bringewoodian (excluding slumps and turbidites) and this is for a relatively minor thickness). This lithology constitutes the non turbidite beds of the 'Wilsonia wilsoni Grits' of Kerry and S.W. Clun (Earp 1938, 1940) and the Bailey Hill Beds of Knighton (Holland 1956, 1959), the non slumped beds of the Striped Flags of the 'Brecon Anticlinal' (Kirk 1948, 1951), the Pterinea tenuistriata Beds of Builth Wells and Cwm Graig Ddû (Straw 1937, 1953), the laminated siltstone facies of Holland & Lawson (1963) and the lower part of the finely flaggy siltstone facies of Bailey (1969).

The lithology consists of tough, brittle, flaggy siltstones

which readily break off as sheets, averaging about 10 mm in thickness (range 5 to 20 mm), along smooth flat bedding surfaces; see Plate 3, Fig. 1. These beds are regularly and finely laminated, with alternate light and dark grey laminae (Plate 2, Fig. 1). Individual laminae can be traced for tens of metres across outcrop without changing thickness.

These laminations are primary as a vertically orientated orthocone shell found in collection B2 from Builth Wells had embedded itself into the sediment disrupting the laminae, laminae deposited later had then banked up against the shell (Plate 2, Fig. 2). In thin section the dark grey and light grey laminae respectively are seen to be composed of clay rich and clay poor silt. The darker laminae contain much dark organic rich clay material, micas orientated parallel to the lamination and relatively minor quantities of fine silt sized, equidimensional, angular to subrounded quartz grains, all cemented by micrite. These laminae average 0.31 mm in thickness (56 measurements, range 0.09 to 2 mm). These darker laminae grade rapidly upwards or downwards into the lighter laminae in which coarse silt sized, equidimensional, subrounded to angular quartz grains are abundant, with relatively rare mica (orientated parallel to the laminations), calcite grains and clay material; all this material is cemented by micrite which is more abundant than in the darker laminae. These lighter laminae average 0.36 mm in thickness (60 measurements, range 0.14 to 2 mm). The average thickness of a pair of laminae is therefore 0.67 mm.

Shells are found sparsely and sporadically in these beds and show no signs of breakage or sorting. The smooth and flat bedding planes and regular lamination show no signs of being disrupted by burrowing. Occasional planes covered by abundant graptolites or P. tenuistriata occur (Plate 2, Fig. 3). Shell debris is absent. Only at Knill do thin (0.5 mm thick) seams of shells, with some shell debris, and fragmented shells occasionally occur. These grade rapidly upwards into the overlying sediment.

Interpretation. Marine 'varved' sediments, identical to those described above, are known from both modern and ancient deposits. Such sediments are found today in Saanich Inlet, British Columbia (Gross et al. 1963), a bay in the S.E. Adriatic Sea (Seibold 1955, 1958), the Santa Barbara Basin off southern California (Hülseman & Emery 1961), the Black Sea (Müller & Blaschke 1969a, 1969b, 1971; Bukry et al. 1970; Ross & Degens 1974; Müller & Stoffers 1974; Emery & Hunt 1974; D. Ross et al. 1978; Stoffers et al. 1978; Degens et al. 1978; Hsü 1978; Dickman & Artuz 1978)

EXPLANATION OF PLATE 2

Sediments Of The Parallel and Irregular Laminated Flags

Fig. 1 Typical appearance of the parallel laminated flags (x 2). Note regular alternations of dark and light laminae; lower Bringewoodian, Knighton. Sample N6.

Fig. 2 Laminae of the parallel laminated flags 'banked up' against a vertically imbedded orthocone shell - indicating primary nature of the laminations (x 3/4); lower Bringewoodian, Builth Wells. Sample B2.

Fig. 3 Top surface of a Pterinea tenuistriata plane (x 3/4); lower Bringewoodian, Cwm Graig Ddû. Sample C31P1.

Fig. 4 Lower surface of a slab of the irregular laminated flags showing trace fossils (x ½); lower Bringewoodian, Cwm Graig Ddû. Sample C34.

Fig. 5 Burrow disrupted laminae of the irregular laminated flags (x 1.1/4); lower Bringewoodian, Cwm Graig Ddû. Sample C30.

Fig. 6 Current disrupted laminae, ripple cross laminated unit of the irregular laminated flags (x 1½); lower Bringewoodian, Cwm Graig Ddû. Sample C27.

Fig. 7 Thin shell bed in the irregular laminated flags (x 2); lower Bringewoodian, Builth Wells. Sample B24S1.

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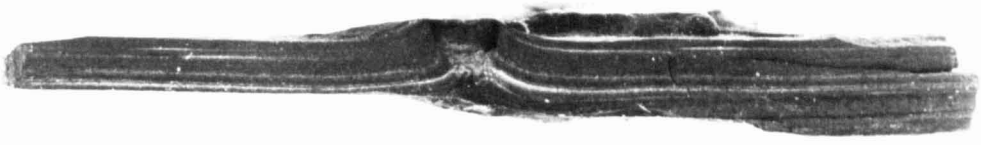

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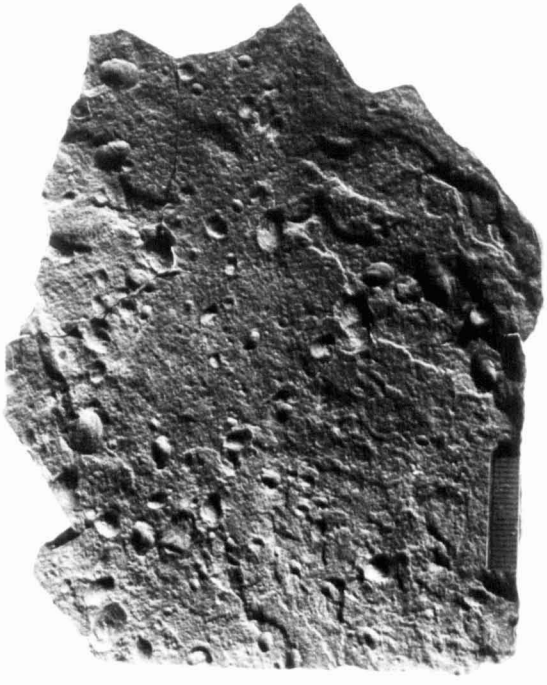

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PLATE 2

and muds of the S.E. Adriatic Sea (van Straaten 1967). Ancient deposits of this type have been described from the Miocene, Pliocene and Pleistocene sediments of the Black Sea (Stoffers & Müller 1978; Stoffers et al. 1978; Hsü 1978; Muratov et al. 1978), from Oligocene bituminous shales and the lower Jurassic Posidonienschiefer (Müller & Blaschke 1969a, 1971), the Posidonienshiefer (Seilacher & Westphal 1971), from the Cretaceous Graneros Shale of the Black Hills region, U.S.A. (Rubey 1930), from Devonian, Carboniferous and Miocene strata (Bradley 1931), from the Triassic of the Southern Alps (Fürsich & Wendt 1977) and from parts of the type Kimmeridge Clay succession (Tyson et al. 1979).

In all these cases the deposits consist of parallel laminated sediments in which light and dark laminae regularly alternate, the modern examples are all found associated with stagnant bottom waters and an absence of bottom fauna and these conditions are therefore presumed to have existed for the ancient deposits too. The absence of benthic forms is due to the low oxygen content of the bottom waters being unable to support life (e.g. Hülseman & Emery 1961; van Straaten 1967; Rhoads & Morse 1971; Pettijohn 1975; Rhoads 1975; Fürsich & Wendt 1977; Stoffers & Müller 1978; Muratov et al. 1978). The presence of the fine uninterrupted laminations testify to deposition below wave base and the absence of benthic forms which destroy this fine bedding by burrowing into and bioturbating it, resulting in 'homogenisation' of the beds (e.g. Dapples 1942; Moore & Scruton 1957; Hülseman & Emery 1961; van Straaten 1967; Rhoads & Morse 1971; Rhoads 1975).

In all of the quoted examples the pairs of laminae (i.e. one light and one dark) are annual in nature with the alternation resulting from seasonal variation in the supply of sediment. The light laminae of some marine 'varved' sediments have been shown to be the products of annual blooms of calcareous or siliceous planktic microorganisms; terrigenous sediment supplied by rivers produces the darker laminae during the rest of the year (e.g. Gross et al. 1963; Hülseman & Emery 1961; Müller & Blaschke 1969a, 1969b, 1971; Bukry et al. 1970; Ross & Degens 1978; Müller & Stoffers 1974; Emery & Hunt 1974; D. Ross et al. 1978; Stoffers et al. 1978; Degens et al. 1978; Hsü 1978). However, other marine 'varved' interbedding is known to arise from seasonal fluctuations in the incoming sediment, so that the coarser layers are deposited as a result of higher rainfall in autumn, winter and spring. An alternation of clay and silt therefore results from varying quantities of these detritals being carried into the water at different times of the year, while

carbonate and silt lamination may be due to seasonal changes in temperature, silt content and salinity of sea water; finally alternations of little or much organic matter are caused by seasonal variation in the quantity of organic matter derived from both the land and the planktic life of the sea (Rubey 1930; Bradley 1931; Seibold 1955, 1958; van Straaten 1967; Dickman & Artuz 1978; Stoffers & Müller 1978; Hsü 1978; Muratov et al. 1978).

Proof of the annual nature of these laminations has been demonstrated in different ways. Hülseman & Emery (1961) and Rubey (1930) worked out sedimentation rates assuming an annual nature for the laminations and found it to be 'normal'. Gross et al. (1963) counted back pairs of laminae down the core to a piece of wood which was then dated (by C^{14}) and found the two figures to agree. Rubey (1930) divided a thickness of laminated strata by the estimated length of time for their deposition and arrived at a figure very close to the thickness of a pair of laminae.

Modern examples of pairs of laminae mostly vary from 2 mm (Hülseman & Emery 1961) to 4 mm (Gross et al. 1963) in thickness, but these figures are for uncompacted sediments. Estimates for compaction of fine sediments vary from 2.6 (Shelton 1962) to 6.0 (Ferguson 1963). An average value of 4.3 was therefore applied to the above modern uncompacted sediments, which suggests that after compaction pairs of laminae would vary between 0.47 and 0.93 mm. These latter figures are comparable with those for the parallel laminated flags (0.67 mm) and ancient marine 'varved' sediments which are commonly 0.5 to 1.0 mm thick (Pettijohn 1976). Therefore, paired laminae of the parallel laminated flags are of the correct thickness to be considered as annual laminations.

To test this hypothesis the thickness of lower Bringewoodian sediments at Cwm Graig Ddû (dominantly of this lithology and with no slumping and turbidite activity during this time to 'distort' the thickness) was divided by an estimate of the time for their deposition. The lower Bringewoodian deposits at Cwm Graig Ddû are estimated to be 248 m thick (the top 35 m are of the irregular laminated flags but the deposition rate was assumed to be the same for these sediments as the parallel laminated flags, in fact the former occasionally show laminae of a similar thickness to the parallel laminated flags). The time range for the Ludlovian is generally believed to be about 10 million years (Ziegler 1970; R. Ross et al. 1978). Assuming each of the 9 divisions of the Ludlow Series represents an equal amount of time, then the Lower Bringewoodian would have lasted 1111111 years. Dividing the 248 m thickness at Cwm

Graig Ddû by 1111111 gives a yearly deposition of 0.2 mm; considering all the assumptions made above, this is broadly comparable with the observed 0.67 mm average for a pair of laminations.

It therefore seems likely that the laminations of the parallel laminated flags were seasonal in nature (as Kirk (1948) tentatively suggested), with the lighter laminae possibly produced in the wet season when rainfall was heavier and rivers could carry more coarse silt material to the basin of deposition, whereas in the dry season only finer silt and clays were removed and deposited. As the coarser silt laminae have a greater pore space than the fine clay rich laminae, the calcareous cement is more abundant in the former.

These beds were deposited in areas beyond wave base and the zone of mixed and aerated surface waters where the bottom waters were not circulated enough to contain sufficient oxygen to support benthic life so that fine alternating laminae from seasonal variations in sediment supply were preserved.

Bailey (1969, p.292) considered that the pale laminae of this lithology were produced by bottom currents carrying sediment from another source. As evidence he quoted measurements of ripple cross lamination, scour features and aligned and current sorted shells. However, all these features are absent from the parallel laminated flags (which as noted above show no signs of bottom current activity, see also data on P. tenuistriata shell size and orientation; p. 123-125); such features are however present in the overlying irregularly laminated flags (p.119-120) which can be easily and clearly distinguished from the parallel laminated flags (Straw 1937, 1953). However because Bailey (1969) lumped these two lithologies (formed in different environments) together, as the finely flaggy siltstone facies, and from evidence of current activity in the upper part of this facies assumed the presence of currents throughout it he came to conclusions that were not applicable to the lower part. These lower strata (the parallel laminated flags) show no signs of bottom currents, which in any case would have brought in oxygenated waters allowing benthic forms to colonise the bottom and destroy the lamination.

Fragmented shells and shell debris in occasional shell beds at Knill suggest short lived turbulent episodes, interrupting the normally quiet environment of deposition. They are very similar to distal storm deposits of the shelf sediments (cf. Tables 3.1 and 4.1) and are therefore considered to be products of very distal storm activity.

Slump Beds

Slumps are found on the western and eastern margins of the north-

SECTION	TOTAL THICKNESS OF STORM BEDS IN m	NUMBER OF STORM BEDS	AVERAGE THICKNESS OF STORM BEDS IN m	TOTAL THICKNESS OF LOWER BRINGEWOODIAN EXAMINED IN m	STORM BEDS PER m OF SECTION	STORM BED % OF LOWER BRINGEWOODIAN
KNILL	0.015	5	0.003	16.77	0.30	0.09
BUILTH WELLS	0.015	3	0.005	82.28	0.04	0.02

Table 4.1 Thickness and frequency of storm deposits in the lower Bringewoodian basin sediments. (cf. Table 3.1).

north-east trending basin in the lower Bringewoodian strata (Fig. 4.1), where they occur interbedded with the parallel laminated flags. At this level they constitute the 'contorted beds' of the Pterinea tenuistriata Beds at Builth (Straw 1937), the 'contorted beds' of the 'Wilsonia wilsoni Grits' of Kerry and S.W. Clun (Earp 1938, 1940), the slump beds of the Striped Flags of the Brecon 'Anticlinal' region (Kirk 1948, 1951), the slump beds of the laminated siltstone facies and the turbidite siltstone facies of Holland & Lawson (1963), the slumped siltstone facies of Bailay (1964, 1969) and the Ludlow slump sequence of Woodcock (1976a, 1976b) and Bailey & Woodcock (1976).

Slumps were found in two of the basinal sections examined in this study, at Builth Wells and Knill which are both situated on the eastern margin of the basin. The following description is based on the slumps in these areas. The slumped masses of siltstone often appear massive, but on close examination are found to be flaggy in nature, beds vary in thickness between 1 and 10 cm, being usually nearer the thinner end of this range. This flaggy bedding reveals the form of the slump folds (Plate 3, Fig. 2). The surfaces of these beds occasionally show crinkle marks (Plate 3, Fig. 4), lineations with a 1 mm to 1 cm spacing, which result from microfolding of a fine sedimentary lamination (Williams & Prentice 1958; Woodcock 1976a). They are usually parallel to the fold hinges of the slump folds. Although the top of slump sheets are usually well defined, they often grade into the unslumped sediments beneath.

These slumped siltstones are usually medium grey in colour and internally homogeneous, however, rarely they are laminated and the laminae then show puckering, and evidence of microfaulting (Plate 3, Fig. 3). In thin section the slumped siltstones consist of mainly equidimensional, subangular to subrounded, silt grade, quartz grains and rare micas cemented by micrite.

The slump folds usually occur as separated noses within an apparently more structureless sediment, as observed also by Woodcock (1976a, 1976b) and Bailey & Woodcock (1976). The folds occur as tight and rounded recumbent folds of the order of tens of centimetres 'high' and 'long' (amplitude and wavelength cannot be measured, since folds occur as isolated noses with no clearly defined inflexion points (Woodcock 1976a)). The structural style of the Ludlow slumps has been described in detail by Woodcock (1976a).

Measurements of the lower Bringewoodian slumps at Knill and Builth Wells show that at Knill the slumped unit is 4.32 m thick and makes

EXPLANATION OF PLATE 3

Slump And Turbidite Sediments

Fig. 1 Typical appearance of the parallel laminated flags in the field. Note regular flaggy bedding; Eltonian, Knill.

Fig. 2 Slumped unit (K12); lower Bringewoodian, Knill.

Fig. 3 Slumped unit showing puckering and faulting of laminae (x 2), cf. Straw (1937, Plate 27, Fig. 1); lower Bringewoodian, Builth Wells. Sample B11.

Fig. 4 Crinkle marks on bedding surface of slump unit (x 1); lower Bringewoodian, Knill. Sample K12.

Fig. 5 Flute on sole of turbidite (x 3/4); lower Bringewoodian, Kerry. Sample D8.

Fig. 6 Turbidite with shelly sole and contorted laminae (x 1); lower Bringewoodian, Kerry. Sample D5.

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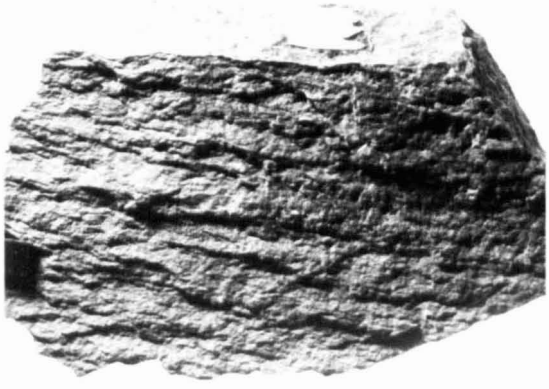

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PLATE 3

up 34% of the division whereas at Builth Wells the average thickness of slumped and interbedded unslumped sediments is 2.7 m (6 measurements) and 6.0 m (7 measurements) respectively, with slumps making up 28% of the lower Bringewoodian part of the P. tenuistriata Beds (whose unslumped sediments consist of the parallel laminated flags). Measurements of mean fold hinge orientation are 091° for Knill (3 measurements) and 064° for Builth Wells (6 measurements); these are plotted on Fig. 4.1. Vergence and facing (Woodcock 1976a, 1976b), when either can be detected, is always to the north west. Folds close in about equal numbers north-west and south-east.

A sparse fauna is found scattered through the sediments of the slumped sheets.

Interpretation. Alternation of slumped and undisturbed units testifies to intermittent downslope mass movement of partially consolidated sediment which was sufficiently cohesive to deform plastically. According to Woodcock (1976a), the gradational lower contacts reflect high shear strains. The presence of slump sheets in the western and eastern boundary regions of the basin confirms the presence of palaeoslopes in these areas; Woodcock (1976b) has argued that slumped masses could not have travelled appreciable distances on a flat trough floor.

The measurements of slumps from Knill and Builth Wells support the conclusions of Cummins (1959b), Bailey (1964, 1969), Woodcock (1976a, 1976b) and Bailey & Woodcock (1976) that slumps in these areas moved down an eastern basin palaeoslope, trending north-east to south-west (from fold hinge axes orientation) and dipping to the north-west (from fold facing and vergence). Although the slumps of the western margin were not visited during this study, Bailey (1969), Woodcock (1976b) and Bailey & Woodcock (1976) have shown, using the same techniques outlined above, that they were deposited on a north-east to south-west palaeoslope facing south-east. The Mongomery Trough model of Cummins (1959b, 1969), Bailey (1964, 1969) and Woodcock (1976b) is therefore confirmed.

The bounding palaeoslopes of the basin appear to be the main site of slump initiation (Cummins 1959b; Bailey 1969). Shocks from fault movement probably provided the triggering mechanism for the slumping of material down these palaeoslopes. The bounding basinal slopes are thought to have been actively controlled by faults which resulted in the greater subsidence of the basin area (Bailey 1969; Ziegler 1970; Woodcock 1976a).

The slumps are considered by Woodcock (1976a, 1976b) to have accumulated at the base of the slope on which they were initiated because

of their inability to travel over the flat basin floor. Supporting evidence for this idea is available in the late Eltonian to early Leintwardinian succession at Cwm Blithus which, from the palaeogeographic reconstructions of Cummins (1959b), Bailey (1964, 1969) and Woodcock (1976b) must represent deposits which lay close to the basin slope - floor break; these have interbedded slumps and unslumped beds of an average thickness of 9 m and 4 m respectively and over 70% of the succession is slumps. Compared with this, in the strata at Builth and Knill, which were deposited much further up the basin slope on the same palaeogeographic reconstructions, slumps are less than half as thick with unslumped units over 50% thicker and slumps making up only about 30% of the succession.

All the fauna contained within a slump is by its very nature transported.

Turbidite Beds

In the lower Bringewoodian turbidites are found in the central axis of the basin, where they occur interbedded with the parallel laminated flags. At this level they constitute the 'grit' bands of the 'Wilsonia wilsoni Grits' of Kerry and S.W. Clun (Earp 1938, 1940) and the Bailey Hill Beds of Knighton (Holland 1956, 1959), the Lower Ludlow Grits of Cummins (1959b), the turbidite siltstone facies of Holland & Lawson (1963) and the silt turbidite facies of Bailey (1964, 1969).

Turbidites were found in two of the basinal sections examined in this study, at Knighton and Kerry. The following description is based on the turbidites in these areas. The turbidite units are medium grey, hard tough, calcareous siltstones which are more resistant to weathering than the enclosing parallel laminated flags and so stand proud of the section as ribs. Their thickness remains constant over outcrop width (up to several tens of metres). The average thickness of turbidites at Knighton was 6.6 cm (57 measurements) and at Kerry was 6.8 cm (259 measurements) although they varied from 3 to 17 cm in thickness. They form 22% of the succession examined at Knighton and 32% of that at Kerry. Alternating and interbedded with these turbidites are units of the parallel laminated flags whose average thickness is 22 cm (60 measurements) at Knighton and 15 cm (255 measurements) at Kerry.

The turbidite beds often show well developed grading which may be emphasised by the concentration of shells in the base of these units (Plate 3, Fig. 6); such shells are always disarticulated and often broken and fragmented. The chaotic nature of the shells in most turbidites results from their rapid settling out of suspension (Middleton 1967),

although, in some turbidites the shells are well orientated e.g. sample DTJ from Kerry. 'Shelly' turbidites are relatively rare comprising only 3.9% and 14.0% of all turbidites examined at Kerry and Knighton respectively. The turbidite beds often show good lamination; laminae are thin (1 to 4 mm) light grey, siltier layers of a rather diffuse nature. These laminations are sometimes parallel to bedding but generally represent low angle cross bedding, they are also quite commonly convoluted (Plate 3, Fig. 6). Flute casts (Plate 3, Fig. 5) are quite common on the soles of many of these beds and indicate the direction of the palaeocurrent which deposited the bed. Measurements of flute marks at Kerry made in this study show remarkably little variation in the flow direction of these palaeocurrents which varied from 320° to 345° with a mean direction of 322° (18 readings), this data has been plotted on Fig. 4.1.

In thin section the turbidites show an abundance of silt grade subangular to subrounded quartz, some clay and some parallel orientated micas with a micrite cement. Laminations are formed by more quartz rich layers.

Interpretation. The above observations and measurements confirm that these hard calcareous siltstones are turbidites which flowed northwards along a relatively flat, narrow basin floor gently inclined to the north, beyond the range of slumps which moved down marginal bounding palaeoslopes to the east and west, as suggested by Cummins (1959b, 1969), Holland & Lawson (1963), Bailey (1964, 1969), Woodcock (1976b) and Bailey & Woodcock (1976).

The reduction in the number of fossiliferous turbidites between Knighton (14.0%) and Kerry (3.9%) is taken to indicate a southerly source area, since the shell fragments are the largest and heaviest sized particles of the turbidite flow and would be deposited first. This is confirmed by palaeocurrents deduced from flute casts on the bases of turbides at Kerry which suggest that their source lay to the south-south-east, possibly on the basinal slopes of the area around Knill. Bailey (1969) has measured the orientation of flute marks in many sections through basinal turbidite sequences of late Eltonian to early Leintwardinian age (Fig. 4.1), which indicate a source area around Knill-Aymestrey-Brampton Bryan (op. cit., p.286). The marked attenuation of the strata of this age (particularly the Bringewoodian) in the Knill-Aymestrey area has been noted by Kirk (1948, 1951), Lawson (in Allender et al. 1960, p.228; 1973a) and Bailey (1969, p.287), see also Fig. 1.2. In fact, the lower Bringewoodian may be only 17 m thick at Knill (p. 104). Such an attenuation is

only to be expected, however, if this area was acting as a source for all the turbidites flowing north-north-west and many of the eastern basinal margin slumps at this time (Bailey 1969, p.287, 297).

The probable initiation of these turbidite flows was by shocks from movement of the fault controlled palaeoslope. These would cause sheets of sediment to slump downslope, some of which disaggregated completely and mixed with water to form turbidite currents which flowed down into the basin and northwards along its axis. Turbidite flows may have 'banked up' and 'overflowed' slumped masses lying at the bases of the basin marginal slopes to give interbedded turbidites and slumps (Woodcock 1976b).

The fauna of the 'shelly' turbidites is obviously transported. Nevasskaya (1978) has described examples of turbidites transporting shells which lived in the shelf area of the Black Sea into the deeper water of the basin centre.

Irregular Laminated Flags

This lithology forms a relatively minor part of the basinal lower Bringewoodian. At Builth Wells and Cwm Graig Ddû it occupies the upper 9.8% (31 m) and 14.1% (35 m) of the lower Bringewoodian respectively. This lithology was mapped as the '<u>Atrypina</u>' Beds at Builth and the Lower <u>Lingula lata</u> Beds at Cwm Graig Ddû (Straw 1937, 1954). It has been included in the laminated siltstone facies of Holland & Lawson (1963) and the finely flaggy siltstone facies of Bailey (1969). The transition between the underlying parallel laminated flags and these strata is rapid in both sections, as noted by Straw (1937, 1953), see also Fig. 4.6.

These sediments do not contain interbedded slumps or turbidites. They are medium grey, tough, brittle, flaggy siltstones, 1 to 2 cm thick. Bedding surfaces frequently show horizontal or low angle burrows (Plate 2, Fig. 4) 2 to 4 mm in diameter and up to 6 cm long. Most of these beds are irregularly laminated, although occasional patches of parallel lamination (identical to those of the underlying parallel laminated flags) are seen. Some beds show no lamination but are very mottled in appearance. The laminations, usually a few millimetres thick, consist of alternating dark grey clayey siltstone laminae and light grey, coarser, more quartz rich and less clay rich laminae. These laminae are virtually identical in composition and texture to those of the parallel laminated flags except the lighter laminae appear coarser, and their description is not repeated here.

These laminae are usually lensed, latterally varying from zero to a few millimetres thick over several tens of centimetres. Laminations are often seen to be disrupted by burrowing (Plate 2, Fig. 5). Also

present are ripple cross laminated beds (Plate 2, Fig. 6), ripples usually have an amplitude of 1 cm and a wavelength of 8 cm.

Other features of this lithology are tool marks and parallel orientated orthocone shells. Measurements of these by the author suggest bottom palaeocurrents moving towards 024° (mean of 22 measurements, range 010° to 034°) at Cwm Graig Ddû and 032° (mean of 28 measurements, range 010° to 040°) at Builth Wells.

Shell beds, generally just a few shells thick, with some included shell debris and coarse quartz grains occasionally occur (Plate 2, Fig. 7). These grade rapidly upwards into overlying sediment. Shells are usually disarticulated and some are fragmented. Measurements of shell beds are given in Table 4.1.

Outside these shell beds, shell debris and fragmented shells are not found and the fauna is of a sparse and fairly sporadic nature.

Occasional occurrences of planes with abundant P. tenuistriata are virtually confined to the lower part of this lithology.

Interpretation. The lack of interbedded slumps and turbidites indicates that mass movement of sediment had ceased in these areas by the time these strata were being deposited and that the tectonic environment was more stable.

The ripple cross laminated beds have also been noted by Straw (1937, p.409) and Bailey (1969, p.292). The constant orientation of ripples, tool marks and orthocones in these strata (recorded by Bailey (1969) and in this study) indicate a remarkably uniform current, which flowed to the north-north-east; suggesting a source area somewhere to the south-south-west probably in the sandy facies of the Llandovery region.

It is considered that the introduction of currents into a previously poorly oxygenated bottom environment caused the water to circulate so that oxygenated water reached the bottom allowing benthic forms to live and burrow into the sediment disrupting laminations and in some cases (as in the mottled beds) completely reworking the sediment (cf. Moore & Scrutton 1957).

The abundance of shell debris and fragmented shells in the shell beds compared to their absence in surrounding sediments suggests short lived very turbulent episodes compared to the normal apparently quiet environment of deposition. The generation of these shell beds may have been from distal storm activity. They are very similar in many respects to deposits interpreted as forming in this way on the shelf to the east of the basin (p.65, 67, 68 and compare Tables 4.1 and 3.1).

Conclusions of Sedimentological Investigations

The lower Bringewoodian of the basinal facies was deposited in a north-north-east orientated fault controlled trough which subsided faster than the surrounding area to accumulate about 4 to 8 times as much sediment as the average (40 m) shelf thickness in the lower Bringewoodian (Fig. 1.2). Since the basin contains slumps and turbidites derived from the shelf edge and upper slope regions its bottom must have been at a greater water depth than that of the shelf, although its exact depth is uncertain.

During most of the lower Bringewoodian the parallel laminated flags were deposited. These sediments are very similar to modern and ancient examples either forming or considered to have formed in poorly oxygenated bottom waters, which excluded benthic life, so that laminations (possibly annual) were not disrupted or destroyed by the activities of benthic animals or currents.

On the palaeoslope margins sediments slumped down and accumulated at the shelf-floor break. Measurements of slumps indicate the presence of eastern and western bounding palaeoslopes which dipped in towards the basin axis, along which turbidite currents flowed north. Palaeocurrents suggest that all the turbidites of this time and many of the eastern margin slumps were derived from the Knill area of the eastern bounding palaeoslope. The derivation of large masses of sediment from this area accounts for the marked attenuation of the lower Bringewoodian succession observed here. Generation of slumps and turbidites was probably from movement along the faults controlling the marginal palaeoslopes of the basin. Such shocks would cause sediment to move downslope towards the axial zone. If it was cohesive it became internally deformed as slump sheets but some disaggregated completely and mixed with water to form turbidity currents which flowed downslope and along the basinal axis.

During the late lower Bringewoodian at Builth and throughout this division at Cwm Graig Ddû mass movement of sediment ceased, indicating a more stable tectonic environment in these areas.

Towards the end of the lower Bringewoodian north-north-east flowing bottom currents apparently from the Llandovery area reached the Builth and Cwm Graig Ddû region and water circulation therefore improved resulting in a more oxygenated bottom environment which benthic forms could and did colonise. Both the bottom currents and the benthic fauna were responsible for disrupting the laminae of these beds, hence the name, irregular laminated flags. Distal storm effects apparently reached these areas occasionally.

A summary of lower Bringewoodian sedimentation patterns in the basinal area is given in Fig. 4.1.

BASIN FAUNA

From the basin area over 12,000 individual specimens representing some 44 species were extracted during this work. The mean relative abundance (see p. 73 for method of calculation) of each species in each section was calculated for faunas occurring sporadically through the sediment, in graptolite or P. tenuistriata bedding plane assemblages, in slumps, in turbidites and in shell layers for each basin lithology (see Tables 4.2 and 4.3). These mean relative abundances helped in the comparison of faunas laterally between sections. Although this method masks vertical changes within one lithology, such variations were examined (see Figs. 4.2 to 4.6). Using data provided in these tables and figures the distribution of fauna within the basin can be examined.

The Distribution Of Individual Taxa ("In Situ" Fauna)

From sedimentological studies (see previous section) it has been deduced that all the fauna found in the basin has been laterally transported, except that occurring sporadically throughout the sediment in the parallel laminated flags and the irregular laminated flags and that of the P. tenuistriata and graptolite plane assemblage. The faunal distribution in all these groups is therefore considered in this section in an attempt to deduce factors affecting the original, primary, distribution of the fauna (i.e. unaltered by lateral transport of organisms). To do this, data on the autecology and environment as derived from functional morphological and sedimentological studies respectively were utilised. The transported faunal assemblages are discussed later.

The distribution of each taxon is outlined in a brief prose description. This is not meant to accurately describe the distribution of each species, since this is given in the tables and figures presented in this chapter, but to emphasise the main aspects.

P. tenuistriata. This species dominates the fauna of the parallel laminated flags. It forms over half the fauna scattered through the sediments in all sections but Knill, where it is uncommon. It is less common in the irregular laminated flags and declines in abundance upwards in this lithology to become a rather rare element of the fauna. In both the former and the lower part of the latter lithology it occurs abundantly and monospecifically as planes of shells covering widely spaced bedding

Table 4.2 Mean relative abundance values for the sporadically scattered fauna P.tenuistriata planes (PP), graptolite planes (GP), shell beds (SH), slump faunas (SL) and turbidite faunas (TU) of the lower Eringewoodian parallel laminated flags

	CWM CRAIG EDU		KNILL				BUILTH WELLS			KNIGHTON				KERRY			
		PP		GP	SH	SL		PP	SL		GP	PP	TU		GP	PP	TU
A.grayi			4.35		73.78	35.10											
A.reticularis									0.87								0.37
C.implicata													0.64				0.38
dalmanellids indet.					0.08								26.33				4.60
D.navicula						17.50			16.70				15.54				16.05
H.elegans									1.82				0.80				0.28
H.canalis									1.10								
I.orbicularis						1.80			4.53								
L.depressa					0.06												
L.lata	7.09		10.43		1.90		8.03			1.35				0.19			
M.nucula	0.82				0.04		1.92		9.67				36.53				32.34
P.minimus					0.44				0.88				0.26				0.27
S.ludloviensis					6.60	3.50							5.81				8.02
S.wilsoni	0.17		0.60		0.08	1.80	7.85		38.15				5.28				21.28
S.euglypha																	0.28
C.cornucopiae			3.88				2.69			5.70				2.52			1.19
C.planulata																	0.27
C.subplanulata									2.87								
L.reticulata																	0.13
P.tenuistriata	88.81	100.00	2.20				66.92	100.00	20.57	54.78		100.00		68.36		100.00	12.45
C.lawsoni					0.98												
D.myops						10.50							0.23				
E.stubblefieldi					0.08												
Proetus sp.									0.48								
P.obconicus					6.74												
beyrichiaceans					7.40	7.00							1.24				0.13
smooth ostracods					1.10	14.00							0.43				
Fistulipora sp.													3.51				0.93
vinculariiform trepostome													1.93				0.22
O.dimidiatum	0.38		1.95		0.12		1.45		1.28								
O.subundulatum	0.69		44.10		0.40	8.80	4.32			10.15				6.27			
graptolites	1.94		32.55	100.00			6.78			28.05	100.00			22.69	100.00		
B.bohemicus										x				x			
B.b.cf.tenuis							x										
P.tumescens	x																
S.chimaera s.l.	x						x										
S.c.semispinosus											x						
S.clunensis														x			
S.incipiens			x								x						
S.varians										x	x						
crinoid ossicles (round)					0.16				0.48				1.49				0.92
TOTAL %	99.90	100.00	100.06	100.00	99.96	100.00	99.96	100.00	99.40	100.03	100.00	100.00	100.02	100.03	100.00	100.00	100.11
TOTAL NUMBER OF SPECIES	7	1	8	1	16	9	8	1	13	5	1	1	14	5	1	1	18
NUMBER OF SAMPLES	20	16	4	1	5	1	13	13	6	6	2	7	8	18	13	2	10
AVERAGE DENSITY	1.6	2468.8	2.5	5200.0	6360.0	9.5	1.6	3023.1	4.9	1.8	3000.0	2771.4	9296.9	1.1	2600.0	3084.6	11555.0
AVERAGE SP. PER COLLECTION	3.3	1.0	6.5	1.0	7.4	9.0	5.6	1.0	6.0	4.0	2.0	1.0	8.3	3.3	1.0	1.0	8.0

	CWM GRAIG DDU		BUILTH WELLS	
		PP		SH
dalmaneilids indet.	2.85			
D.navicula	19.52		39.81	76.47
H.elegans				0.97
H.canalis	0.56		0.49	
I.orbicularis	0.38			
L.lata	18.05		6.49	
M.nucula	3.27		6.30	2.77
S.ludloviensis				0.97
S.wilsoni	5.54		35.70	15.03
brachiopod indet.			0.39	
C.cornucopiae	5.22			
P.tenuistriata	36.84	100.00	3.83	
Fistulipora sp.				0.97
O.dimidiatum	1.42			
O.subundulatum	3.25		4.39	2.77
P.ibex	0.38			
graptolites	2.67		2.60	
S.chimaera s.l.	x			
TOTAL %	99.95	100.00	100.00	99.95
TOTAL NUMBER OF SPECIES	13	1	9	7
NUMBER OF SAMPLES	10	2	7	3
AVERAGE DENSITY	2.4	2500.0	4.3	2500.0
AVERAGE SP. PER COLLECTION	6.0	1.0	5.0	3.7

Table 4.3 Mean relative abundance values for the sporadically scattered fauna, P.tenuistriata planes(PP) and shell beds(SH) of the lower Bringewoodian irregular laminated flags.

planes (Plate 2, Fig. 3). In both occurrences the shells are mostly disarticulated, although articulated examples are found suggesting, at most, the activities of minor currents only.

Straw (1937, p.413) inferred that the planes of P. tenuistriata shells were "carried in by currents and spread over the sea floor like a carpet", the reason for this statement was that "a single slab of rock shows a preponderance of either right or left valves" (op. cit., p.413). During field studies it was noted, contrary to Straw's observations, that both left and right valves occurred in about equal proportions on any one P. tenuistriata planes. To verify these findings 5 of these planes, from Builth Wells (collections B6P1 and B17P2), from Cwm Graig Ddû (C18P1 and C22P1) and from Kerry (D5P1), were collected and brought back to the laboratory for detailed study (these were the best examples found; preservations is generally poor). Tests by the χ^2 method revealed no significant difference from at 1:1 ratio for left:right valves in all five cases (Table 4.4). Size frequency graphs (Fig. 4.7) in all five cases show a strong peak at smaller sizes (in fact even smaller shells apparently exist, but due to poor preservation these cannot be measured) and a large size range, usually from less than 1 mm to over 7 mm and up to 12.7 mm. There appear to be about equal numbers of each valve in each size class for all planes (Fig. 4.7). Measurements of umbo orientation (Fig. 4.8) are random in all five cases.

P. tenuistriata occurs abundantly in the sole of a turbidite at Kerry and this collection (DTJ) was also examined for comparative purposes. This sample shows a bell shaped size frequency distribution, with abundant large sized shells, an absence of small and medium sized ones and an unequal number of opposite valves in each size class (Fig. 4.7). A χ^2 test reveals a significant departure from a 1:1 (left:right valve) ratio (Table 4.4). Orientation measurements show that umbones are preferentially aligned (Fig. 4.8).

Boucot (1953), Olson (1957) and Fagerstrom (1964) have argued that a 'life assemblage' may be recognised by an abundance of small individuals, while a bell shaped size frequency distribution will indicate a 'death assemblage,' with the small shells having been removed by currents. However, Rigby (1958), Craig & Hallam (1963), Craig & Oertel (1966), Hallam (1967) and Craig (1967) have shown that the primary shape of size frequency graphs depends on the interaction of different growth and mortality rates (and possibly also, to a lesser extent, recruitment); a bell shaped distribution therefore is not necessarily indicative of a

SAMPLE NUMBER	NUMBER OF LEFT VALVES (% IN BRACKETS)	NUMBER OF RIGHT VALVES (% IN BRACKETS)	TOTAL NUMBER OF VALVES IN SAMPLE	χ^2 TEST
B6P1	147 (54.6 %)	122 (45.4 %)	269	NO SIGNIFICANT DIFFERENCE FROM A 1:1 RATIO (RV:LV)
B17P2	80 (51.6 %)	75 (48.4 %)	155	
D5P1	67 (58.3 %)	48 (41.7 %)	115	
C18P1	85 (54.5 %)	71 (45.5 %)	156	
C22P1	46 (52.9 %)	41 (47.1 %)	87	
DTJ	41 (85.4 %)	7 (14.6 %)	48	SIGNIFICANT DIFFERENCE FROM A 1:1 RATIO (RV:LV)

Table 4.4 Proportion of left valves (LV) and right valves (RV) and results of χ^2 tests to determine whether there is a significant difference from a 1:1 ratio (RV:LV) in various P.tenuistriata rich samples. All samples are from P.tenuistriata planes except DTJ which is from the sole of a turbidite.

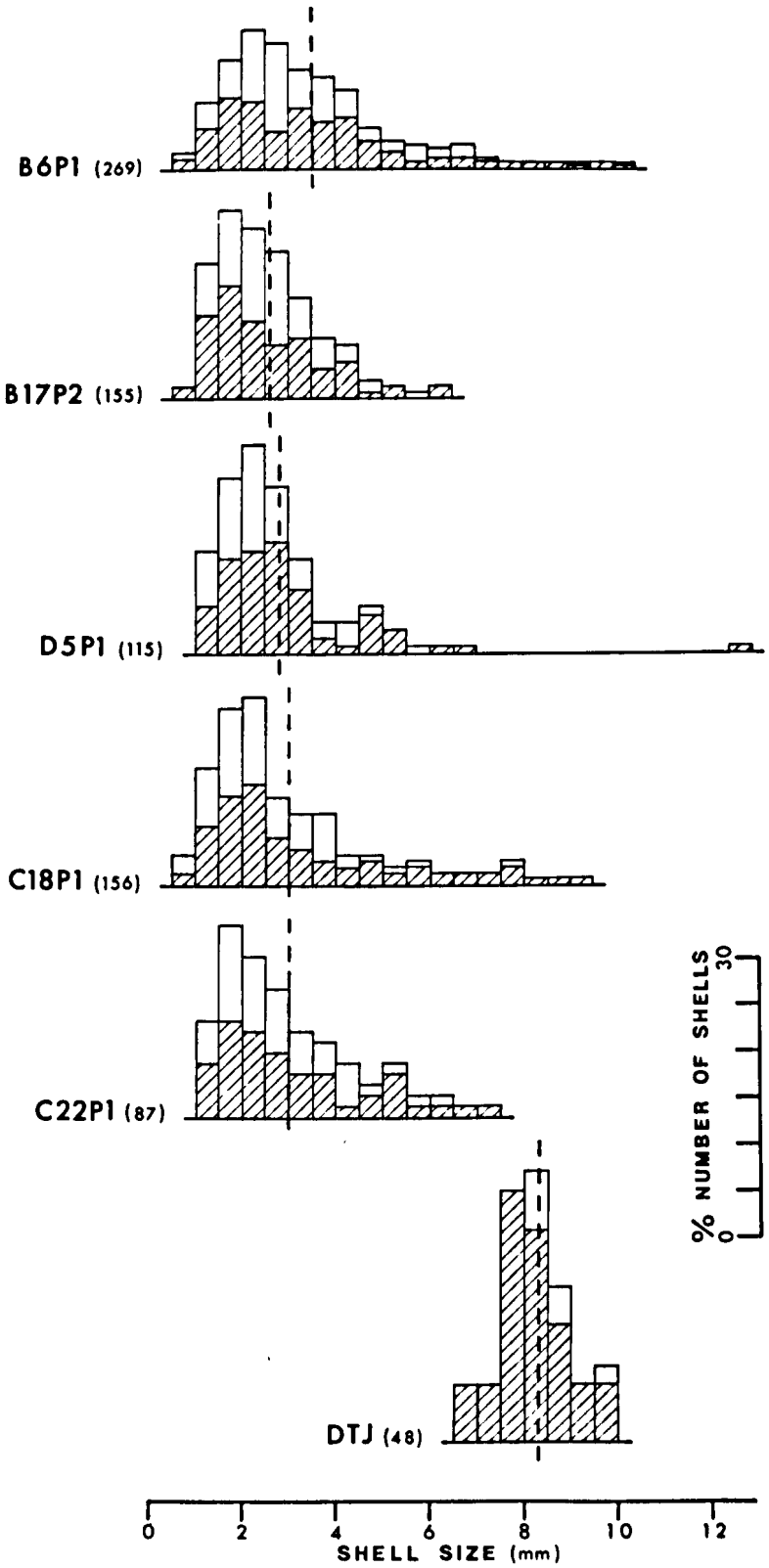


Fig. 4.7 Size frequency histograms , showing mean size (vertical bars) for 6 collections of Pterinea tenuistriata from 3 localities, Builth (B) , Kerry (D) and Cwm Graig Ddu (C) in the parallel laminated flags of the lower Bringewoodian. All collections are from P.tenuistriata planes except DTJ which is from the sole of a turbidite. Shell size is measured as the maximum length of the shell from the umbo. Histograms are standardised to 100 individuals to aid comparison ; actual number of shells in each sample are given in parentheses. Shaded areas indicate measurements of left valves , unshaded areas indicate measurements of right valves.

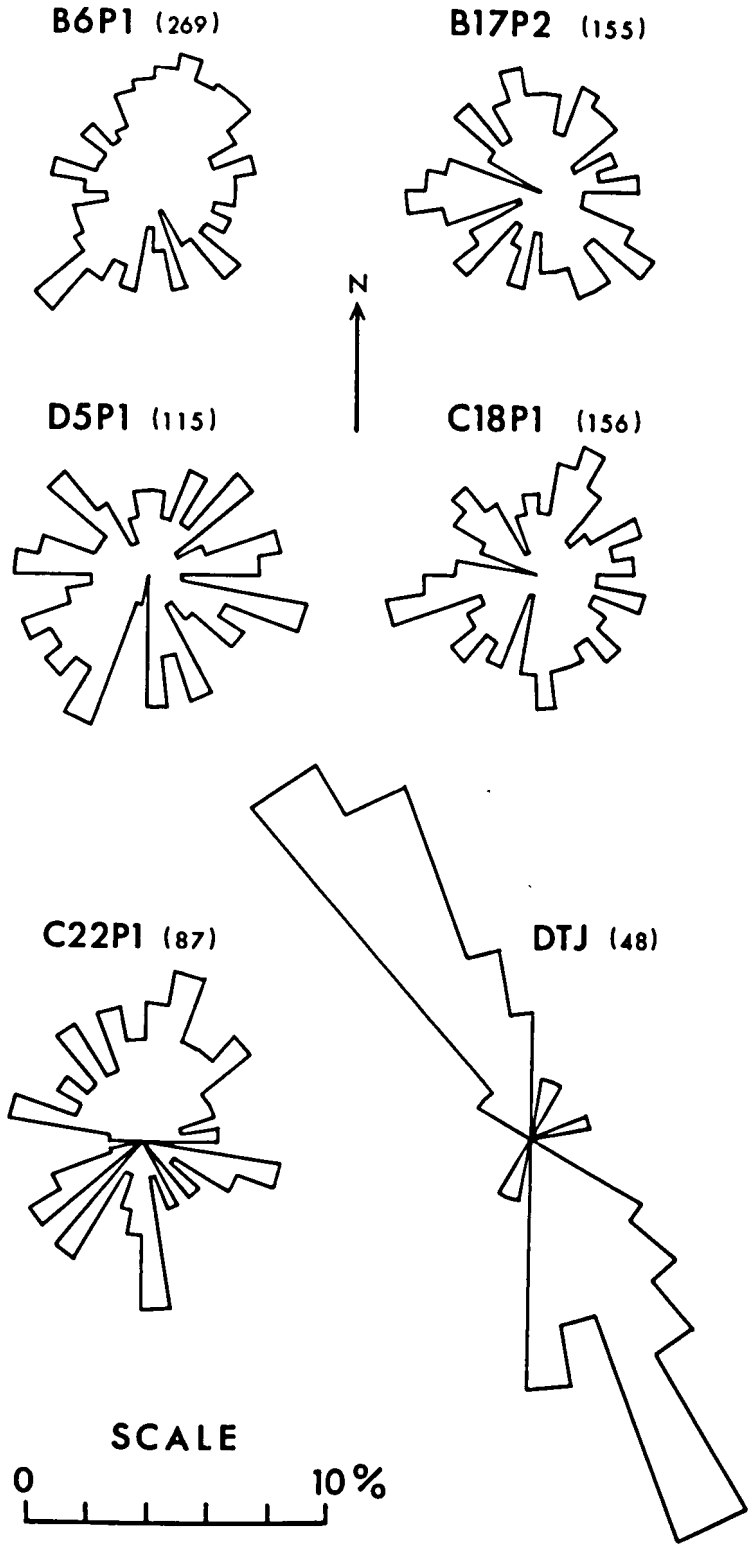


Fig. 4.8 Orientation of Pterinea tenuistriata umbones in 6 collections of P. tenuistriata from 3 localities, Builth (B), Kerry (D) and Cwm Graig Ddu (C) in the parallel laminated flags of the lower Bringewoodian. All collections are from P. tenuistriata planes except DTJ which is from the sole of a turbidite. Class intervals are 10°. Diagrams are standardised to 100 individuals to aid comparison. Actual number of shells in each sample are given in parentheses.

'death assemblage'. Although Craig & Oertel (1966, p.351) note that most of the organisms studied by ecologists so far appear to have constant or decreasing rates of mortality which must produce greater numbers of small dead individuals than large. Brookfield (1973) suggested a bell shaped size frequency distribution may arise from adults excluding larval settlement, but Thayer (1975a) rejected this hypothesis and explained the lack of small shells by recruitment failure due to patchy larval distribution.

Evidence for the removal of small shells (probably by fragmentation) is overwhelming e.g. Menard & Boucot (1951), Newall (1966), Hallam (1967), Trewin & Welsh (1972) and Worsley & Broadhurst (1975). Craig & Hallam (1963, p.745) argued that although it was undeniable that directional currents were capable of sorting shells their presence should not be assumed just because of a bell shaped distribution.

The presence of many small shells and a large size range has been shown by various authors to correspond to very low current activity and hence a lack of selective destruction of small shells (Boucot 1953; Fagerstrom 1964; Broadhurst 1964; Hallam 1967, p.41).

Therefore although the presence of a bell shaped size frequency distribution does not necessarily equate with a current winnowed 'death assemblage', since it may arise from varying rates of recruitment, growth and mortality, the presence of many small shells and a large size range is indicative of either very weak currents or their absence. Therefore the 5 P. tenuistriata planes examined appear to have all been preserved in a very quiet environment; while the absence of small shells in the turbidite sample (DTJ) may not be the result of current sorting their position in the sole of a turbidite suggests this is the most likely explanation.

Lever & Thijssen (1968, Martin-Kaye (1951) and Craig (1967) all noted that current action tended to produce a marked sorting of opposite bivalve valves due to their different hydrodynamic properties. Boucot (1953), Boucot et al.(1958) and Craig & Hallam (1963) have all argued that current undisturbed assemblages will have identical numbers of each valve in each size category. This is true for the 5 P. tenuistriata planes but not for the turbidite sample; this indicates lack of current sorting in the former and extensive selective transport in the latter involving the preferential removal of right valves.

Kelling & Williams (1967), Nagle (1967) and Brenchley & Newall (1970) all showed that shells become orientated in currents although shell

size, weight, substrate type etc. affect the orientation relative to the current. The random umbo orientation of the 5 P. tenuistriata planes suggests a lack of current activity which was responsible for aligning the shells in the turbidite sample (DTJ), since the umbos are aligned along the direction of current flow as deduced from flutemarks (p. 118).

It is therefore concluded that contrary to Straw's (1937, p.413) statement the 5 P. tenuistriata planes examined show no signs of current activity; this suggests an extremely quiet environment of deposition. If currents had been present in this environment then the assemblages would have shown features like that of the turbidite sample.

Evidence discussed on p.25-26 suggests that P. tenuistriata was epiplanktic, attached to floating algae. The latter eventually sank to the bottom carrying its attached fauna with it into a quiet environment of deposition in which no currents capable of disturbing them were present; this suggestion accords with the sedimentological evidence. The quiet continuous nature of basinal deposition makes it extremely unlikely that P. tenuistriata planes represent breaks in deposition. The lack of size sorting suggests that the algae must have floated down with the P. tenuistriata shells still attached, otherwise they would have become sorted as they settled through the water column. The occurrence of sporadic valves throughout the succession probably represent individuals dislodged in the surface waters. The rarity of this species on the shelf may result from fragmentation of the small thin valves in the more turbulent waters of the shelf, or from an original distribution pattern centred on the basinal area and possibly related to some feature of the surface water environment. Its decline in abundance, in the lower irregular laminated flags, to its eventual rarity suggests the former hypothesis, since the waters of the shelf environment are thought to have been more turbulent.

Recently Kauffman (1978a, 1978b) has claimed that sparse episodic bivalve faunas from the Jurassic Posidonienschiefer and the Solnhofen and Nusplingen Limestones of Germany, interpreted as epiplanktic forms in oxygen depleted basins (Seilacher & Westphal 1971), are in fact benthic. Kauffman considers that these bivalves lived on such surfaces as the shells of dead ammonites elevated above the poorly oxygenated bottom waters during periods of partial oxygenation. As Kauffman (1978b) and Brenner & Seilacher (1978) have argued, such periods of oxygenation and associated current activity, which aligned belemnites and sometimes allowed a low density fauna of opportunistic benthic species to colonise, were short episodes compared to the background situation in which benthic life was

not possible due to a low degree of oxygenation. Such conditions cannot explain the P. tenuistriata planes since they are not found encrusting elevated surfaces, such as orthocone shells, and no evidence of currents, such as aligned shells, to produce such oxygenated episodes are present.

Graptolites. Graptolites are one of the commonest elements of the fauna in the parallel laminated flags, forming 20% to 30% of the fauna in all sections except at Builth Wells (about 7%) and Cwm Graig Ddû (about 2%), although they are still the fourth and third most abundant taxon respectively. In this lithology they occasionally occur as masses of rhabdosomes covering bedding planes. In the irregular laminated flags graptolites are less common.

Since graptoloids lived suspended below gas filled vacuolated tissue in the uppermost water layer (p.31-33) and since the faunal density per unit volume is approximately the same in all basin sections for the parallel laminated flags, though the proportion of graptolites changes, the decrease of graptolites seen at Builth Wells and Cwm Graig Ddû must be real and not an artifact. This cannot be explained by 'sediment dilution' since the lower Bringewoodian successions at Kerry and Knighton (in which graptolites are abundant) are of a similar thickness to the lower Bringewoodian successions at Builth and Cwm Graig Ddû (in which graptolites are rare). This feature also cannot be the product of selective preservation (Rickards 1975) which is thought to be responsible for their rarity in the shelf sediments (see p. 82), since from sedimentological studies it is considered that the same extremely quiet bottom environment existed at this time at all basin localities. Watkins & Berry (1977) have suggested that different environments in different surface water masses (one favourable to graptolites over the basin and one less favourable over the shelf) could explain graptolite distribution, although they did not consider selective preservation (see p.33). However, as Watkins & Berry (1977, Fig. 7) show the 'graptolitic water mass', during the Bringewoodian, existing over all the basin localities examined this cannot explain their distribution either. The reason remains enigmatic but it is possibly due to some feature of the surface water environment. The decrease of graptolites in the irregular laminated flags is however probably directly related to the increased turbulence of the bottom water environment which would have destroyed, by fragmentation, a greater proportion than in the underlying parallel laminated flags (see p.32). The planes of graptolites are probably due to the sinking of gregarious masses, since the quiet continuous nature of basin sedimentation makes it extremely unlikely that they represent breaks in deposition.

Lingula lata. This species occurs scattered throughout the parallel

laminated flags and the irregular laminated flags in all sections and is quite common, except in the parallel laminated flags at Kerry and Knighton, in the axial region of the basin, where it is relatively rare. It is therefore commonest in the sediments deposited on the palaeoslopes of the basin. The author has found it articulated perpendicular to bedding apparently *in situ* in both facies, it is therefore a burrowing species and not epiplanktic as Watkins & Berry (1977) suggested. Cherns (1977, 1979) also records *L. lata* apparently in its burrow from the basinal Lower Leintwardine Beds. Lockley (pers. comm. 1977) has also found this species articulated and perpendicular to bedding in the irregular laminated flags at Cwm Graig Ddû.

L. lata therefore apparently lived in the basinal sediments even in the parallel laminated flags, which are considered to have been deposited in conditions of poorly oxygenated bottom waters, which excluded all other benthos. However, Cloud (1948) has noted that lingulids appear to have a preference for, and are well adapted to, conditions of low oxygenation and occur in muds "blackened and ill smelling from the decomposition of organic matter" (*op. cit.* p.244). Therefore *L. lata* may well have been well adapted to the low oxygen concentration of the bottom waters of the basin. It could also probably stand the high turbidity and constant sedimentation (Thayer & Steele-Petrović 1975) of this environment (see p.23-24). The rarity of *L. lata* in the axial region of the basin may reflect very low levels of oxygenation which were inadequate for its survival.

Orthocones. The small smooth forms '*O'. dimidiatum* and '*O'. subundulatum* are quite commonly scattered throughout the parallel laminated flags (being commonest at Knill) and the irregular laminated flags. The large ornamented form *P. ibex* is confined to the latter lithology where it occurs rarely.

The large ornamented forms such as *P. ibex* are thought to have been nektobenthic predators and scavengers (see p.34) and therefore their absence from the parallel laminated flags probably indicates the absence of their prey (benthic fauna) which appear to have been excluded by poorly oxygenated bottom waters. The small smooth forms were probably nektic living in the surface waters amongst the algae, attached epiplanktic taxa and graptolites (see p.34) on which they may have preyed.

The presence of unimploded orthocones in the basinal sediments indicates water depths of less than 600 m according to Westermann(1973,

1977). However Saunders & Wehman (1977) have urged caution in the determination of water depths from fossil cephalopods (p.33-34).

Cardiola cornucopiae. This species occurs uncommonly but consistently, scattered through the basinal sediments in all sections except the parallel laminated flags at Cwm Graig Ddû and the irregular laminated flags at Builth. The species is probably epiplanktic (p.26) which explains its presence in the former lithology which is thought to have been deposited in poorly oxygenated bottom waters. Its wide distribution occurring, albeit rarely, in both basin and shelf facies is supporting evidence for its presumed epiplanktic mode of life.

S. wilsoni and M. nucula. Both these species occur uncommonly, scattered through the parallel laminated flags deposited on the basin palaeoslopes (i.e. where slumps are present in the succession), however they are absent from this lithology in the axial region of the basin. Both species are more common in the irregular laminated flags and at Builth S. wilsoni is particularly in this lithology.

The presence of similar rhynchonellid brachiopods (Leiorhynchus and Camarotocchia) in sediments considered to have been deposited in bottom waters too low in oxygen to support benthic life (Sutton et al. 1970), can be explained by the ripping up of algal fronds, on which these species may have lived in shelf waters, by currents which transported them out into the basin waters in which they finally settled (Bowen et al. 1974; and see p.15). Ager (1962, 1965) and Thayer (1974) have suggested that rhynchonellids found in sediments without other benthic forms may have been epiplanktic. However, both these species appear to have been benthic, possibly living attached to algal fronds in quite turbulent environments (p.15-16). It is extremely unlikely that they could have lived in the poorly oxygenated waters of the parallel laminated flags or have thrived abundantly in the very distal conditions represented by the irregular laminated flags. Their presence in these lithologies is therefore explained by benthic algae, to which they may have been attached, being ripped up by currents and carried into marginal basin areas. Their absence from the Kerry and Knighton regions is possibly because these areas lay beyond the range of such algae transporting currents.

A. grayi. This species occurs sparsely scattered in the parallel laminated flags at Knill. A.grayi may have been either epiplanktic or benthic living on algae in the shelf edge region (p.21-22). Its presence in sediments considered to have been deposited in poorly oxygenated bottom

waters can therefore be explained either by an epiplanktic life style or, alternatively by the same 'shelf algae attachment' hypothesis outlined above.

D. navicula and H. canalis. Both species are confined to the irregular laminated flags. D. navicula is the commonest member of the fauna in this lithology while H. canalis occurs sporadically and rarely. Their absence from the parallel laminated flags is probably due to the low oxygen content of the bottom waters in which these were deposited. These species are both well adapted to quiet water conditions (p.20) and are thought to have lived in the quiet waters associated with the irregular laminated flags. D. navicula appears to have been far more successful than H. canalis.

I. orbicularis and dalmanellid indet. Although absent from the parallel laminated flags these occur rarely and sporadically in the irregular laminated flags. Since I. orbicularis is not adapted to quiet environments (p.18) this accounts for its rarity in the irregular laminated flags. Its absence from the parallel laminated flags was probably due to the low oxygen content of the bottom waters.

Transported Assemblages

The fauna of these assemblages was not discussed in the previous section, since an attempt was being made to determine the factors which affected the original, primary, distribution of the fauna. Transported assemblages in the basinal lower Bringewoodian are found in slumps, turbidites and in shell lenses which may be the result of distal storm activity. By comparing the fauna of these transported assemblages with that of the 'indigenous' fauna of the shelf and basin some idea of the degree of transport may be obtained. About 20 species out of the 44 found in the basin are confined to transported assemblages, emphasising the low diversity of the 'indigenous' basin fauna.

Slumps at Knill contain an abundance of D. navicula and A. gravi together with other benthic forms such as ostracods and trilobites. This fauna contrasts with the graptolite and orthocone dominated 'indigenous' fauna (Fig. 4.2). A fauna similar to the former one was not observed on the shelf during this study but as D. navicula and A. gravi are both quiet water distal shelf forms (p.20 and p.21) it is possible that these species dominated an outermost shelf fauna. Sediments from this environment then slumped down the palaeoslope. The abundance of D. navicula, S. wilsoni and P. tenuistriata in the slumps at Builth contrasts with the 'indigenous'

fauna (Fig. 4.5) suggesting transport from another environment, which must have been similar to that in which the irregular laminated flags were deposited, where a comparable fauna can be found. Again slumping appears to have been from an outermost shelf or marginal basin environment. The P. tenuistriata in these slumps may have been from this environment or may have been incorporated from the local parallel laminated flags (in which they are abundant) during slumping.

'Shelly' turbidites at Knighton and Knill are variable in faunal composition but the fauna is usually of a diverse benthic kind including brachiopods, bivalves, bryozoans, trilobites etc. unknown from the 'indigenous' fauna of the surrounding parallel laminated flags lithology. Sorting during transport, fragmentation of smaller and more fragile shells and the incorporation of fauna from other localities along the path of the turbidity current have probably altered the faunal composition considerably, and also affected the diversity. The concentration of the fauna into the base of turbidites has increased the faunal density immensely. However, it can be stated that the turbidites originated in an area with a rich benthic fauna, which, from the palaeocurrent evidence of flutes, must have lain shelfwards of the Knill area (p. 118). Again the abundance of D. navicula suggests an area of the outermost shelf in which this species was abundant, but such an area, with this fauna, is not exposed at present. Some of the turbidites, however, have been derived from the basinal sediments because they contain a basinal fauna e.g. sample DTJ in which P. tenuistriata dominates and benthic forms are absent.

Shell layers in the irregular laminated flags at Builth have a fauna which is similar to that scattered through the surrounding sediment, suggesting that transport was limited and may have been very minor. The fauna of the shelf layers in the parallel laminated flags at Knill is completely different from that of the surrounding sediments suggesting transport from a different environment, the abundance of benthic forms in these shell beds indicates a more favourable environment than that of the surrounding sediments with their mainly pelagic fauna. The abundance of ostracods and A. gravi in these deposits, which are both considered to have lived on benthic algae, suggests that storms may have ripped up such algae from a shelf edge locality and transported it, together with other benthic forms, into the basin. All these shell layers are considered to have been produced by the distal effects of storms (p. 114, 120).

Again we can see that the recognition of transported assemblages is important, since a sample from them may give an erroneous indication of the original habitat and presence or abundance of a taxon when it was alive.

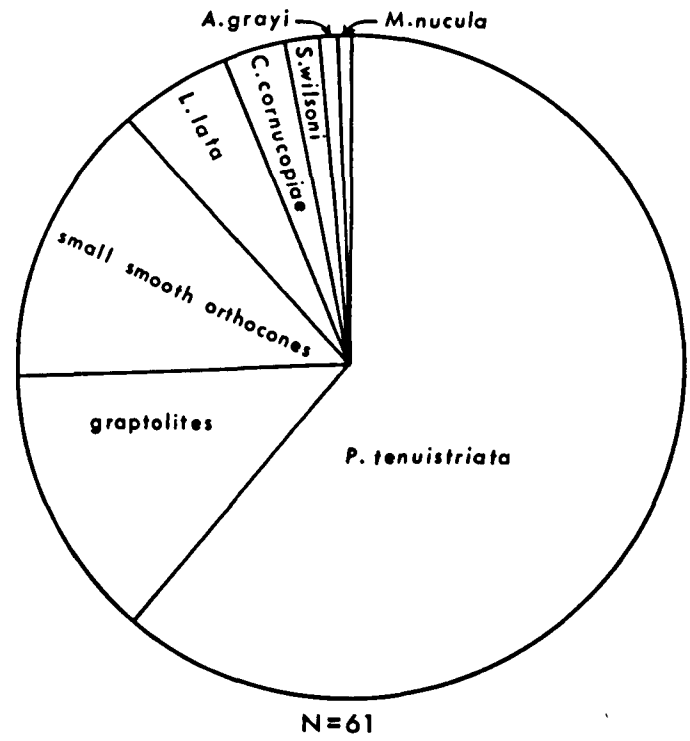
Faunal Assemblages In The Basin

It has been shown that by examining the functional morphology of individual taxa and the sediments in which they were found it is possible to explain the distribution of fauna in the basinal sediments. Further information may be gained by the recognition of faunal assemblages. Faunal assemblages from the basinal lower Bringewoodian have not been recognised or described before. Data for these are derived from the fauna scattered through the strata, but not from the extensively laterally transported faunas of the slumps, turbidites and distal storm deposits or the graptolite and P. tenuistriata planes, which are described above. Lateral and vertical faunal variation within one sediment type is not very marked and the main changes are between different sediment types.

Descriptions of each assemblage are brief since all the details are summarised in the tables and figures presented in this chapter. Descriptions are based on the fauna in the lower Bringewoodian parts of these lithologies only. Although both the parallel laminated flags and the irregular laminated flags are known to extend beyond the confines of this division, they are not discussed further. Density is given as the average number of individuals per 5000 cm^3 of sediment for each assemblage. Diversity is given as the average number of species per collection for each assemblage (since insufficient numbers for rarefraction to 100 individuals were obtained).

Basin Assemblage 1. This is the fauna of the parallel laminated flags which is dominated by P. tenuistriata, graptolites and orthocones in all sections (the former two may occur crowded on bedding planes). Less common to rare forms are C. cornucopiae, L. lata, S. wilsoni, M. nucula and A. gravi. Density is consistently very low (1.1 to 2.5) and diversity very low (3.3 to 6.5), especially when these are compared with figures of about 30 and 10 to 15 respectively, which were considered low values on the shelf.

Basin Assemblage 2. This is the fauna of the irregular laminated flags which is dominated by D. navicula, L. lata and S. wilsoni, C. cornucopiae, M. nucula and orthocones being less common, but still relatively



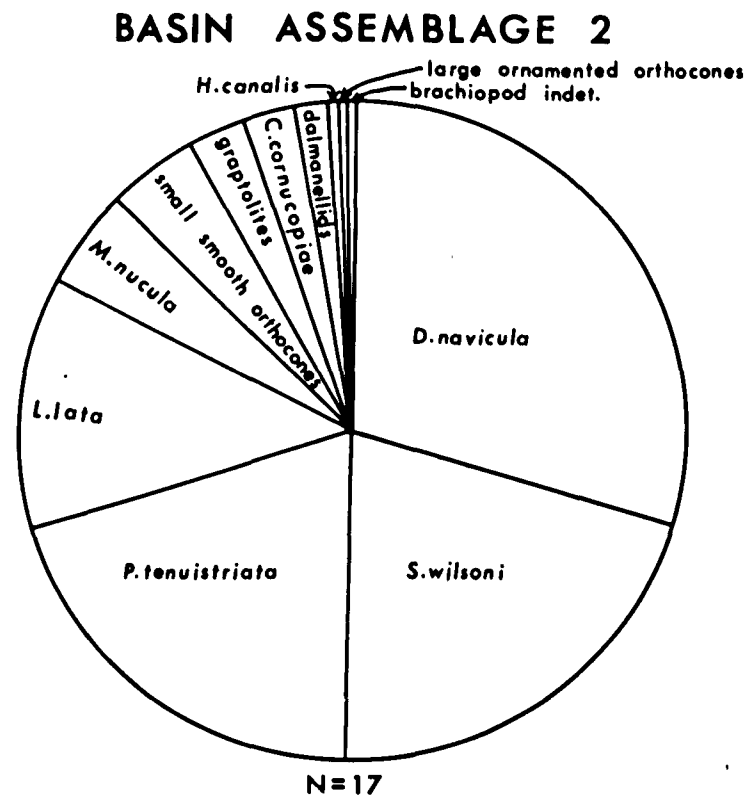


Fig. 4.9 Abundance of taxa in each lower Bringewoodian basin assemblage. N = Number of samples used in compiling each diagram. Graptolite and P.tenuistriata planes not included.

numerous. The fauna is both denser (2.4 to 4.3) and more diverse (5 to 6) than 'Basin Assemblage 1' but all the values are low compared to the shelf assemblages.

Fig. 4.9 illustrates the composition of both basinal assemblages.

Factors Controlling Faunal Distribution In The Basin Facies

In this study all the morphological adaptations of each taxon, as well as all the environmental parameters, as deduced from a study of the sediments, were considered before the most important controlling factors of both were inferred. From such an approach it proved possible to explain the observed distribution of each lower Bringewoodian basin taxon. A similar approach is now adopted to explain the distribution of each basinal faunal assemblage.

During deposition of the parallel laminated flags the basin floor was below the level of normal circulation. Bottom currents were absent. Therefore oxygen was not effectively renewed in these bottom waters and due to oxidation of organic matter and respiration the amount of dissolved oxygen fell to the level where almost all benthos was excluded. Due to the absence of benthic forms and currents, laminations (possibly annual) were preserved. These sediments are identical to modern and ancient examples either forming or considered to have formed in very poorly oxygenated bottom waters.

The fauna of recent oxygen deficient marine basins has been studied by Rhoads & Morse (1971). They found that well calcified benthic forms are restricted to environments with a level of dissolved oxygen of at least 1.0 ml/l. Below this level and down to about 0.3 ml/l only an impoverished fauna of small worms survives. Levels below 0.1 ml/l exclude virtually all macrofaunal benthos.

The fauna of the parallel laminated flags has been interpreted here as either holoplanktic (graptoloids), nektic (orthocones) epiplanktic (P. tenuistriata and C. cornucopiae), epifaunal, attached to benthic algae which have been uprooted and transported into the basin waters (S. wilsoni, M. nucula and A. grayi), and infaunal, in basin sediments (L. lata). Therefore the latter appears to be the only truly indigenous benthic form in these sediments.

Such a fauna is not atypical of basins with a low oxygen level in their bottom waters. Kennet & Penrose (1978) have recently described modern examples of calcareous polychaetes attached to Sargassum like seaweed from anoxic basin sediments, thereby indicating the importance of

epiplanktic rafting in contributing a preservable fauna to a depositional environment hostile to life. Thayer (1974) and Ager (1962, 1965) have evoked epiplanktic rafting to explain the presence of brachiopods in strata considered to have been deposited in very poorly oxygenated bottom waters. Rhoads (1975) has stressed the importance of epiplanktic rafting in delivering a fauna into anoxic basins. Bowen et al. (1974) have discussed recent and fossil examples of fauna attached to benthic algae being transported into basins with low oxygen levels in the bottom waters.

It can therefore be seen that almost every major group of benthic taxa was excluded by the poorly oxygenated bottom conditions existing during the deposition of the parallel laminated flags. Articulate brachiopods, bivalves, gastropods, trilobites, bryozoa , echinoderms, corals, ostracods and worms, all present to abundant on the shelf, were excluded. Only one species (an inarticulate brachiopod, L. lata) could tolerate the low oxygen levels of this environment. Cloud (1948) has shown that some species of Lingula are very tolerant of very low oxygen levels. Therefore the fauna of the parallel laminated flags reflects the very low levels of dissolved oxygen in bottom waters. This is not to suggest that they were anoxic, but that the level of dissolved oxygen in the bottom waters was below the level tolerated by virtually all benthos, i.e. about 0.1 ml/l (Rhoads & Morse 1971).

During the deposition of the parallel laminated flags, turbidite currents, slumps and storms periodically brought shelf edge sediments and a displaced rich benthic fauna into the basinal areas (the turbidites into the basin centre, and the slumps and storm deposits onto the marginal palaeoslopes).

The change from deposition of parallel laminated flags to irregular laminated flags, towards the end of the lower Bringewoodian at Cwm Graig Ddû and Builth is marked by an abrupt and rapid change in fauna and facies with little transition between the two. It appears that the cause was the sudden arrival of north-north-east flowing bottom currents which improved water circulation and led to an oxygenated bottom environment, and presumably also brought in food. This allowed benthic forms (other than L. lata) to colonise. Although the results of current activity are obvious in these sediments, conditions appear to have been very quiet, with distal sedimentation and oxygen levels still relatively low. The restricted, low density and low diversity indigenous benthic fauna reflects such conditions. This fauna consisted of worms which

disrupted the sediments (e.g. Moore & Scrutton 1957), L. lata, H. canalis, dalmanellids and D. navicula. The latter form dominated this indigenous benthic fauna, whose members show good adaptations to quiet water conditions. The small size of the individuals in this assemblage means they could probably tolerate low food and oxygen levels (see p.20). Other forms were non benthic; P. tenuistriata and C. cornucopiae were epiplanktic, graptolites were holoplanktic and orthocones were nektic (the presence of ornamented orthocones (nektobenthic) probably reflects the presence of an indigenous benthic fauna on which they may have preyed). M. nucula and S. wilsoni probably lived attached to shelf benthic algae which were uprooted and transported into basin waters.

Conditions were therefore still unfavourable for most benthic forms. However the presence of an indigenous shelly benthos suggests dissolved oxygen levels must have been higher than in the underlying parallel laminated flags, although still comparatively low compared to most of the shelf.

During deposition of the irregular laminated flags distal storm effects reached the area. However turbidites and slumps were absent indicating a more stable tectonic environment.

Sanders & Hessler (1969), Johnson (1970, 1971), Rhoads & Morse (1971), Dörjes (1972), Jackson (1972) and Cisne & Rabe (1978) have all shown that faunal gradients reflect environmental gradients. Johnson (1972) has argued that if environmental gradients are gradual then communities will change gradually, but if sharp breaks exist in the environmental gradient then communities will appear discontinuous. Therefore during the lower Bringewoodian, in the basin there were two extensive periods, during which the environment was very stable, so that the fauna remained largely similar, between which the environment suddenly changed. The sudden arrival of bottom currents into previously poorly oxygenated, uncirculated waters is thought to have been responsible.

The difference in diversity between the two basin assemblages can be explained in terms of greater physiological stress in one environment reducing diversity relative to the other, as noted by workers on modern faunas (Sanders 1968, 1969; Slobodkin & Sanders 1969; Sanders & Hessler 1969; Johnson 1970, 1971; Jackson 1972; Stanton & Evans 1972). Such stress was high in both environments but greater in the extremely poorly oxygenated environment in which the parallel laminated flags were deposited. The low faunal diversities in the basin are extensions of the trend in the lower Bringewoodian from a 'middle' shelf high of 22.8 at Ludlow, to 11.0 at the shelf edge (Aymestrey) to 6.5 in the marginal basin area (Knill) to a basin centre low of 3.3 at Kerry. All figures are for the average number of species per collection in the dominant shelf lithology (bioturbated siltstone facies) and the dominant basin

lithology (parallel laminated flags). This decrease in diversity is obviously due to a stress gradient from the poorly oxygenated bottom waters of the basinal environment to the well oxygenated and mixed waters of the middle shelf. With the highest directed physiological stress in the former environment and the least stress in the latter. Sanders (1968) and Rhoads & Morse (1971) have also noted that along a gradient of decreasing dissolved oxygen, diversity decreases. The reduction in dissolved oxygen with increasing depth has been evoked to explain the decline in diversity of species in an offshore direction in the Late Cretaceous of South Dakota by Rhoads et al. (1972) and to explain the same trend in the Devonian of New York State (Sutton et al. 1970; Bowen et al. 1974; Thayer 1974). Workers on modern faunas have also noted that diversity changes along a stress gradient, with the highest diversities in the lowest stress environments (Sanders 1968; Sanders & Hessler 1969; Johnson 1970, 1971; Jackson 1972).

The degree of physiological stress is also thought to have controlled faunal density, with the lowest densities in the poorly oxygenated bottom waters of the parallel laminated flags. Sutton et al. (1970), Bowen et al. (1974) and Thayer (1974) came to identical conclusions in an examination of the Devonian of New York State. With improved water circulation, but still high stress conditions, in the irregular laminated flags faunal density increased but was still comparatively low compared to shelf values. Therefore factors limiting the number of individuals also appear to have limited the number of species.

Conclusions

A complex of physical environmental factors interacted to control the distribution of the basinal taxa. Since bottom currents were inactive and because active tectonic subsidence of the floor of the fault controlled trough had taken it beyond the reach of normal surface circulation, the bottom waters in which the parallel laminated flags were deposited were very poorly oxygenated, which excluded virtually all benthic forms. The only indigenous benthic form (L. lata) not only had to be tolerant of such poorly oxygenated conditions, but also of constant sedimentation and high levels of turbidity.

Late in the lower Bringewoodian because bottom currents brought in more oxygenated and food rich waters more benthic forms could colonise. However, the quiet water, distal shelf conditions probably meant reduced oxygenation and food supply (relative to the shelf for example) to which only a few species could adapt. In this environment the irregularly laminated flags were deposited.

CHAPTER 5

THE LLANDOVERY TO LLANDEILO AREA - SECTIONS, FACIES AND FAUNA

RECOGNITION OF THE LOWER BRINGEWOODIAN

The most recent authors mapping the Llandovery-Llandeilo area (Price 1957; Potter 1960; Potter & Price 1965; Squirrell & White 1978) have all noted the difficulty of correlating the succession here with the type area at Ludlow. This is because graptolites are rare, the endemic shelly fauna was strongly influenced by the atypical 'sandy' conditions and the lateral stratigraphical relationship of this area with the graptolitic basinal succession is uncertain.

Potter & Price (1965) correlated the Upper Elton Beds with the middle third of the Black Cock Beds, the Lower Bringewood Beds with the top third of the Black Cock Beds (excluding the Carn Powell Facies and its lateral equivalents) and the Upper Bringewood Beds with the Carn Powell Facies (and its lateral equivalents) plus the Trichrûg Beds and their lateral equivalents the Lower Cwm Clŷd Beds. These correlations were based mainly on elements of the shelly fauna which appeared to be less influenced by the 'sandy' nature of the sediments.

Recently, however, Squirrell & White (1978) have discovered graptolites in the Cennen Valley section which indicate that the Coed Wenallt Beds (the Black Cock Beds, excluding the Carn Powell Facies equivalents of Potter & Price (1965)) to within 50 m of the top of this unit are of nilssoni Zone age and therefore are probably equivalents, in this area, of the middle Elton Beds. The top 50 m of the Coed Wenallt Beds may therefore be equivalents of the Upper Eltonian, the Grammysia Beds (the Carn Powell Facies equivalents of Potter & Price 1965) may correlate with the Lower Bringewoodian, and the Trichrûg Beds with the Upper Bringewoodian. Since Potter & Price (1965) have correlated the various successions within the Llandovery-Llandeilo region this correlation scheme can be extended to the other sections of this area examined in the present study (Fig. 5.1). Such a scheme is rather attractive since the upper Eltonian, lower Bringewoodian and upper Bringewoodian strata of this area would (in each section) have been deposited in successively shallower water conditions (see evidence later), an identical situation to the type area at Ludlow. (Such sea level changes may be regional, due to local tectonic warping, or possibly eustatic, although due to correlation problems the latter case would be difficult to prove.) Supporting evidence for this proposal comes from the uppermost Coed Wenallt Beds which have yielded an upper Eltonian palynological assemblage (Dorning

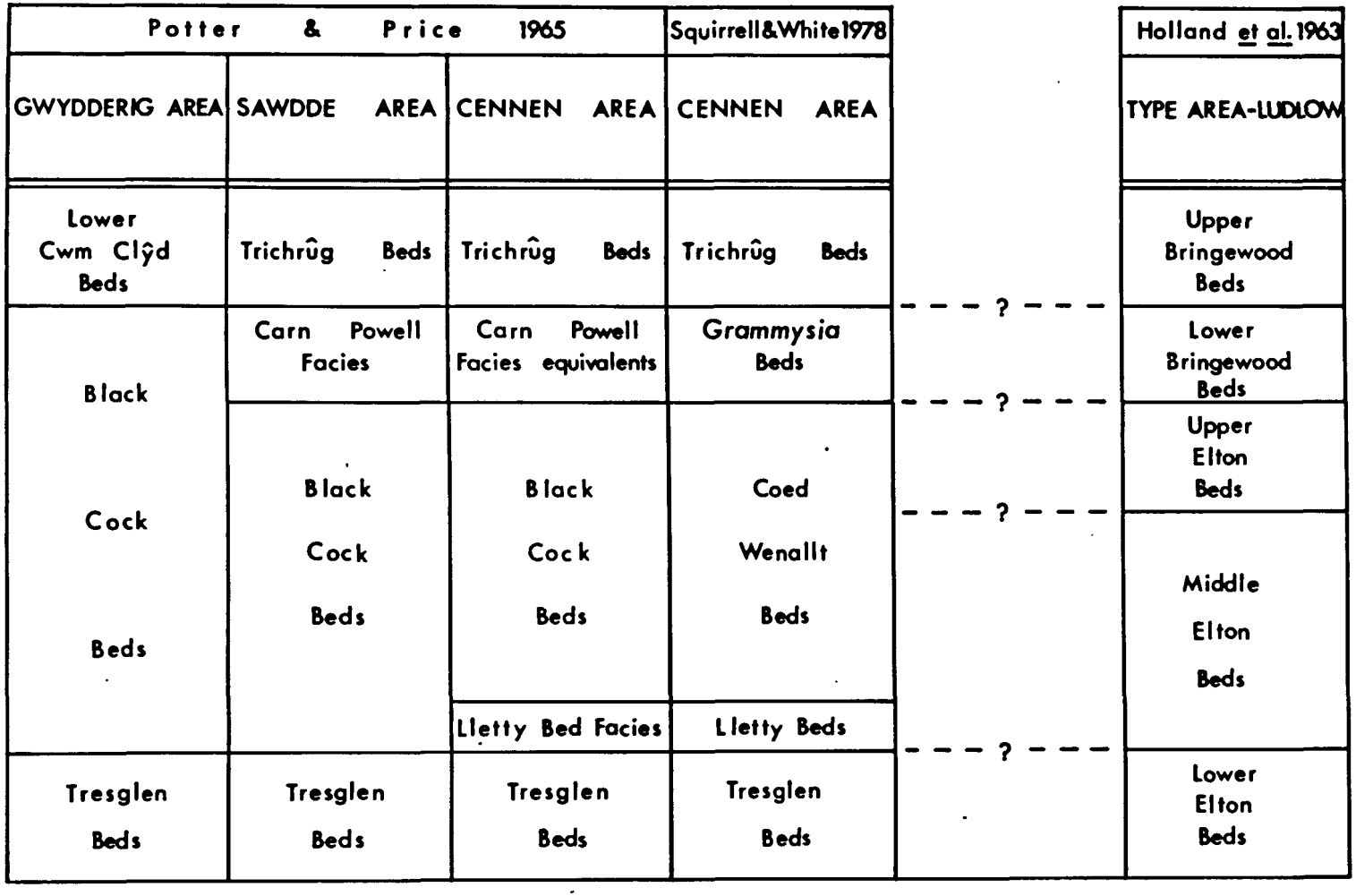


Fig. 5.1 Tentative correlation chart for the lower Ludlovian between the type area and the stratigraphical successions erected for the various sections in the Llandovery - Llandeilo area.

pers. comm. 1978). Obviously due to the lack of any positive evidence (such as graptolites or ostracods) to confirm the correlation of the Grammysia Beds with the lower Bringewoodian, the correlation scheme as shown in Fig. 5.1 must remain unproven. As Squirrell & White (1978, p.14) note, the Grammysia Beds may correlate with either the lower Bringewoodian and or the upper Eltonian. However, from the above discussion, the former correlation is considered more likely.

In conclusion it is considered that the Grammysia Beds (the lateral equivalents of the Carn Powell Facies of Potter & Price 1965) of the Cennen Valley, (thickness 27 m), the Carn Powell Facies of the Sawdde Valley (thickness 39 m) and the, 'equivalent', top 33 m of the Black Cock Beds of the Gwydderig Valley (i.e. the average thickness of the Carn Powell Facies or their equivalents in the Sawdde and Cennen sections) are of approximately lower Bringewoodian age. However, this cannot be proven at present, although, it is the best correlation given the available data. It is hoped that work on palynology and ostracods may soon make correlation in this area more accurate.

SETTING

Holland & Lawson (1963) referred the Eltonian to Leintwardinian strata of this region to a shelly siltstone and a deltaic facies. Potter & Price (1965) noted that the typical features and lithologies of the basin facies, which lies to the north-east, are not developed and that the strata of this region are more representative of a sandy variety of the shelf facies; hence the previous references in this work to a sandy facies existing in this area.

The environmental setting of the strata in this area has been established by Price (1957), Potter (1960), Holland & Lawson (1963) and Potter & Price (1965). Potter (1968, 1977) has also commented briefly on the depositional environment of the Trichrûg Beds. The conclusions of these authors regarding strata considered to be upper Eltonian to Bringewoodian in age (Fig. 5.1) are outlined below.

The blue grey fossiliferous flaggy siltstones of the upper Black Cock Beds of the Gwydderig section (including the lateral equivalents of the Carn Powell Facies), the upper Coed Wenallt Beds of the Cennen Valley and the blue grey fossiliferous coarse siltstones and fine sandstones of the Lower Cwm Clŷd Beds of the Gwydderig section were all considered to represent relatively shallow marine environments (Price 1957; Potter 1960).

The thick, massive, greenish grey and brownish grey sandstones interbedded with thin greenish grey siltstones and mudstones recorded from the Grammysia Beds of the Cennen Valley were also interpreted as shallow marine shelf deposits (Potter 1960).

Thick, wedge bedded, massive or occasionally graded sandstones, interbedded with rippled and cross bedded, greenish grey siltstones and mudstones were recorded from the upper Black Cock Beds of the Sawdde section (Price 1957; Potter 1960; Potter & Price 1965). These were considered by Price (1957) to represent tidal flats with sand deposited in shallow tidal channels. Potter (1960) rejected this idea in favour of one in which floods of sediment were discharged from the mouth of a river and deposited as wedged sandstone units in an area of very shallow, possibly not fully saline water. From the wedging direction of the sandstone units and cross bedding measurements Potter (1960) considered that currents probably came from about 150°; land was thought to have existed nearby in this direction (Price 1957; Potter 1960).

Purple, occasionally cross bedded sandstones which commonly contain pebbles as stringers and lenses within them, and alternate with purple and greenish grey shales were recorded from the Carn Powell Facies of the Sawdde section (Price 1957; Potter 1960; Potter & Price 1965). These sediments were considered by Price (1957) and Potter (1960) to have been deposited on a broad flat alluvial plain (Potter 1960). Current bedding and other sedimentary structures indicate that currents came from about 177° (Potter 1960). The submaturity of the sediments was taken by Potter (1960) to indicate the proximity of this environment to a moderately high land area, possibly in the region of the South Wales Coalfield. Analysis of pebbles and mineral fractions indicated that this provenance area was one of sediments and low grade metamorphics; while heavy mineral analyses indicated deposition in semi-arid conditions, with rapid erosion, transport and burial of sediments (Potter 1960). The purple red colour was considered to be primary and to indicate an oxidising depositional environment, in mainly subaerial conditions (Price 1957; Potter 1960). Some of the sedimentary structures were considered to have been produced by tidal waters advancing over the low lying plain (Potter 1960).

The Trichrûg Beds were noted by Price (1957), Potter (1960, 1968, 1977), Holland & Lawson (1963) and Potter & Price (1965) to consist of thick, unfossiliferous, coarse, cross bedded, pebbly quartzitic sandstones and conglomerates, with interbedded thin shales and sandstones which could be pebbly. Wedging of the coarser units and cross bedding measure-

ments were considered to indicate deposition from about 184°, although heavy mineral assemblages and pebble size analyses indicated a sediment supply from the south-west as well (Potter 1960). These analyses also suggested that the area of provenance was not far from the area of deposition (Potter 1960). The area of provenance to the south-west appeared to have risen up during deposition of the lowermost Trichrûg Beds. The whole provenance area therefore lay to the south and south-west (Price 1957; Potter 1960). In the Cennen Valley Potter (1960) and Potter & Price (1965) commented on the pale cream colour of most of these strata, with few red beds. The bimodal texture of these sediments suggested to Potter (1960) that they were alluvial gravel deposits. The fact that the two sections through these strata on either side of the Cennen Valley, although only 500 m apart, could not be correlated, even with heavy mineral assemblages, was also noted by Potter (1960) and was interpreted by him as a feature of immature sedimentation associated with fluvial deposition. These sediments were therefore considered to have been deposited as wedges of sand and gravel on a broad alluvial plain, close to the area of provenance (Potter 1960; Potter & Price 1965). Rapid burial of the sediment under fluvial conditions was considered responsible for the non-red colour (Potter 1960). In the Sawdde, however, Potter (1960) drew attention to the fact that the quartzites, conglomerates and thin interbedded sediments of the Trichrûg Beds were all red, rarely wedge bedded and unimodal. Such features were considered by Potter (1960) to indicate a depositional environment of braided rivers depositing more sorted material under subaerial and strongly oxidising conditions on a delta plain. Deposition at this time over most of the Llandovery-Llandeilo area, to within a few kilometres of the Gwydderig section, is considered to have been above sea level on the deltaic plain (Price 1957; Potter 1960, 1968, 1977; Holland & Lawson 1963; Potter & Price 1965).

Therefore assuming the correlations of the previous section (Fig. 5.1) are correct then we can summarise the events proposed by these previous workers as follows. During the upper Eltonian, deposition occurred in shallow marine conditions throughout the Llandovery-Llandeilo area. The shallowest water conditions existed in the Sawdde area which appears to have been situated either near the mouth of a river flowing from the south, or consisted of tidal flats. In the lower Bringewoodian shallow marine conditions appear to have persisted in the Gwydderig and Cennen areas but the Sawdde region now constituted a subaerial alluvial or deltaic plain on which rapidly eroded sediments, from an area to the

south, were quickly deposited in very shallow, probably tidal, waters. By upper Bringewoodian times the shallow marine shelf conditions persisted only in the Gwydderig area; to the south-west of this region lay the delta front. The whole area from the Sawdde to the Cennen Valley was above sea level and formed a delta plain which received sediment from a range of hills lying nearby to the south and south-west of the Cennen Valley.

Owen (1967) has suggested that the source of the quartzose pebbles, seen in many of the rocks discussed above, were basal Cambrian conglomerates and quartzites being eroded from an area in the region of the present South Wales Coalfield. Potter (1960), however, noted from analyses of pebbles and mineral fractions that the area of provenance was supplying low grade metamorphics to the Sawdde area during Carn Powell Facies deposition, suggesting the underlying Pre-Cambrian rocks had been exposed in the source area at this time and not later, in the Downtonian, as Owen (1967) has suggested.

Throughout the Eltonian and Bringewoodian to the north-east of the Llandovery-Llandeilo area marine conditions continued without interruption. The sediments get finer to the north-east and appear to have been deposited in quieter and deeper waters towards the basin. R. Marsh (1976) examined the sediments of the area immediately south-west of Cwm Graig Ddû to within a few kilometres of the Gwydderig section, and found evidence, mainly from chemical analyses of the sediments and mineral assemblages that these sediments had been brought in by mainly fluviatile processes from the deltaic outpourings to the south. Therefore the influence of the delta on sedimentation was widespread.

Compared with the rapid change between the basin and shelf facies on the eastern flanks of the basin the boundary between the basin and sandy facies appears to be gradational. R. Marsh (1976) suggested that this was due to the boundary fluctuating throughout time. However, here, it is considered more likely that the absence of a fault controlled slope at this southern end of the basin was responsible for the more gradational change between these two major facies types.

LLANDOVERY-LLANDEILO SECTIONS

Each of the sections examined during this study is considered in turn. The lithological and faunal variation through each section, the position of each sample collected, the density and diversity of each collection and the position of stratigraphic boundaries are shown in the summary charts (Figs. 5.3 to 5.5). A key to the symbols used in these

SHALE

IRREGULARLY FLAGGY SILTSTONES (INCLUDES THIN BEDS OF FINE GRAINED SANDSTONE AND SHALE IN THE SAWDDE SECTION)

IRREGULARLY FLAGGY COARSE GRAINED SILTSTONES AND FINE GRAINED SANDSTONES

MEDIUM GRAINED SANDSTONES

COARSE GRAINED SANDSTONES

CHANNEL IN MEDIUM GRAINED SANDSTONES

CHANNEL WITH MEDIUM GRAINED SANDSTONE FILL IN IRREGULARLY FLAGGY SILTSTONES

SHELLS IN BASE OF MEDIUM GRAINED SANDSTONE UNIT

SHELL BED

* * * * TURBIDITE UNIT

JUNCTION BETWEEN STRATIGRAPHICAL UNITS SEEN

IRREGULAR JUNCTION BETWEEN STRATIGRAPHICAL UNITS SEEN

JUNCTION BETWEEN STRATIGRAPHICAL UNITS UNSEEN OR UNCERTAIN

uB? upper Bringewoodian ?

lB? lower Bringewoodian ?

uE? upper Eltonian ?

DENSITY NUMBER OF INDIVIDUALS PER 5000 cm^3 OF SEDIMENT

Sp.NUMBER NUMBER OF SPECIES PER COLLECTION

DIVERSITY NUMBER OF SPECIES PER 100 INDIVIDUALS

Fig. 5.2 Key to symbols used in Figs. 5.3 to 5.5

charts is given in Fig. 5.2. As each section is discussed, its geographic location, position of sample sites and criteria used for placing stratigraphical boundaries are discussed.

i) Gwydderig

The section investigated in the valley of the Afon Gwydderig is a road cutting on the north side of the A40, approximately 7 km east-south-east of Llandovery. This section was described by Price (1957) and Potter & Price (1965) who established the most recent stratigraphy for this area. The results of this author's investigation of the section are summarised in Fig. 5.3.

The section examined commences at SN 83733250 in the upper Black Cock Beds, some 58.3 m below the base of the Lower Cwm Clŷd Beds, as taken by Price (1957) and Potter & Price (1965), where the base of a feature runs down the valley and crosses the road at SN 37773244. The junction is not exposed but appears to occur just below the lowest exposed strata of the Lower Cwm Clŷd Beds, which are seen at the latter grid reference. This agrees with the maps and descriptions given by Price (1957) and Potter & Price (1965). The base of the Lower Cwm Clyd Beds is therefore taken at the base of sample G13 and the strata between the above two grid references were sampled. Exposure is not continuous and only 35.07 m of strata are exposed out of the 58.31 m estimated to be present in this section. The basal 6 m of the Lower Cwm Clŷd Beds were also sampled.

The Black Cock Beds here consist of a series of micaceous blueish to greenish grey, 2 to 5 cm thick, irregularly flaggy siltstones showing abundant ripple cross lamination and extensive bioturbation. Occasional shell lenses and sharp based medium to fine grained, parallel laminated, cross laminated or graded sandstone units up to 12 cm (but averaging about 6 cm) thick also occur. The latter were called 'grits' by Price (1957). The fauna of these upper Black Cock Beds occurs throughout all the lithologies discussed, except for the sandstones which are unfossiliferous - although, for the sake of clarity, this is not shown in Fig. 5.3. The dominant elements of the fauna are A. reticularis and I. orbicularis, although L. filosa and S. wilsoni may be common at certain levels.

The Lower Cwm Clŷd Beds are very different to the Black Cock Beds, consisting of blue grey, micaceous, 2 to 5 cm thick, irregularly flaggy coarse siltstones and fine sandstones which are ripple cross laminated

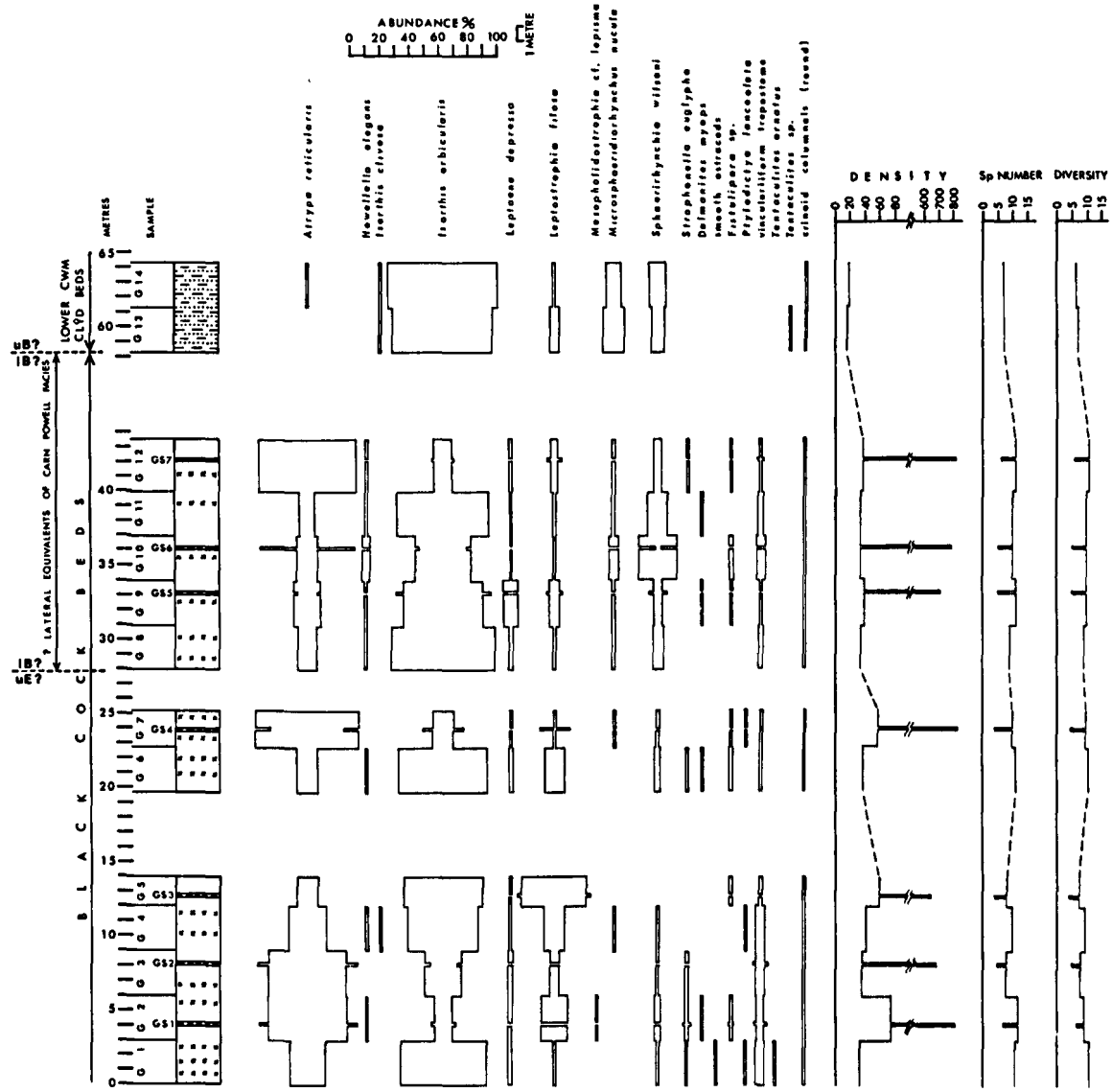


Fig. 5.3 The upper Eltonian and Bringewoodian succession and fauna in the Gwydderig Valley

and bioturbated. The sharp based sandstone units are absent from these strata. However, thin lenses of quartz granules up to 4 mm in diameter are present. Coquinas were observed in the Lower Cwm Clŷd Beds but were not seen in the small section examined in detail. As noted by Price (1957) and Potter & Price (1965) A. reticularis is now relatively uncommon compared to its occurrence in the underlying Black Cock Beds.

As discussed previously (p.136,137) the top 33 m of the Black Cock Beds in the Gwydderig section are considered to be lateral equivalents of the Carn Powell Facies and are possibly lower Bringewoodian in age. The Lower Cwm Clŷd Beds have been shown by mapping to be lateral equivalents of the Trichrûg Beds (Price 1957; Potter 1960; Potter & Price 1965).

ii) Sawdde

The section investigated in the valley of the Afon Sawdde was in the Cwar Glâs Quarries, some 4 km south-south-east of Llangadog. The section has been described by Price (1957), Potter (1960) and Potter & Price (1965) who established the most recent stratigraphy for the area. The succession examined was from some 31.3 m below the base of the Carn Powell Facies, in the upper Black Cock Beds at SN 72652483 to some 3 m above the base of the Trichrûg Beds at SN 72732477, the stratigraphically highest strata exposed in the quarry. Continuous exposure is present between these two grid references. The results of the author's investigation of the section are summarised in Fig. 5.4.

The upper Black Cock Beds consist of a series of bioturbated, micaceous, greenish grey and blue grey, shales, lenticular bedded siltstones and thin fine grained sandstones whose surfaces are covered with mud draped wave and interference wave ripples. Coquinas are also seen. Interbedded between these sediments are coarser, medium grained, sharp based sandstones which appear massive at first but on careful examination show grading, sometimes from a basal layer of shells, parallel lamination and cross lamination. Channels are seen cutting through all of these sediments. The fauna is largely confined to the shell beds but extensive collecting has revealed rare sporadic fossils on the surfaces of the thick sandstone beds and throughout the finer grained units. Although the thick sandstones are almost entirely unfossiliferous throughout their thickness (except for a shell bed or the odd crinoid ossicle at the base of some), this is not shown on Fig. 5.4 for the sake of clarity.

The base of the Carn Powell Facies on Potter's (1960) definition

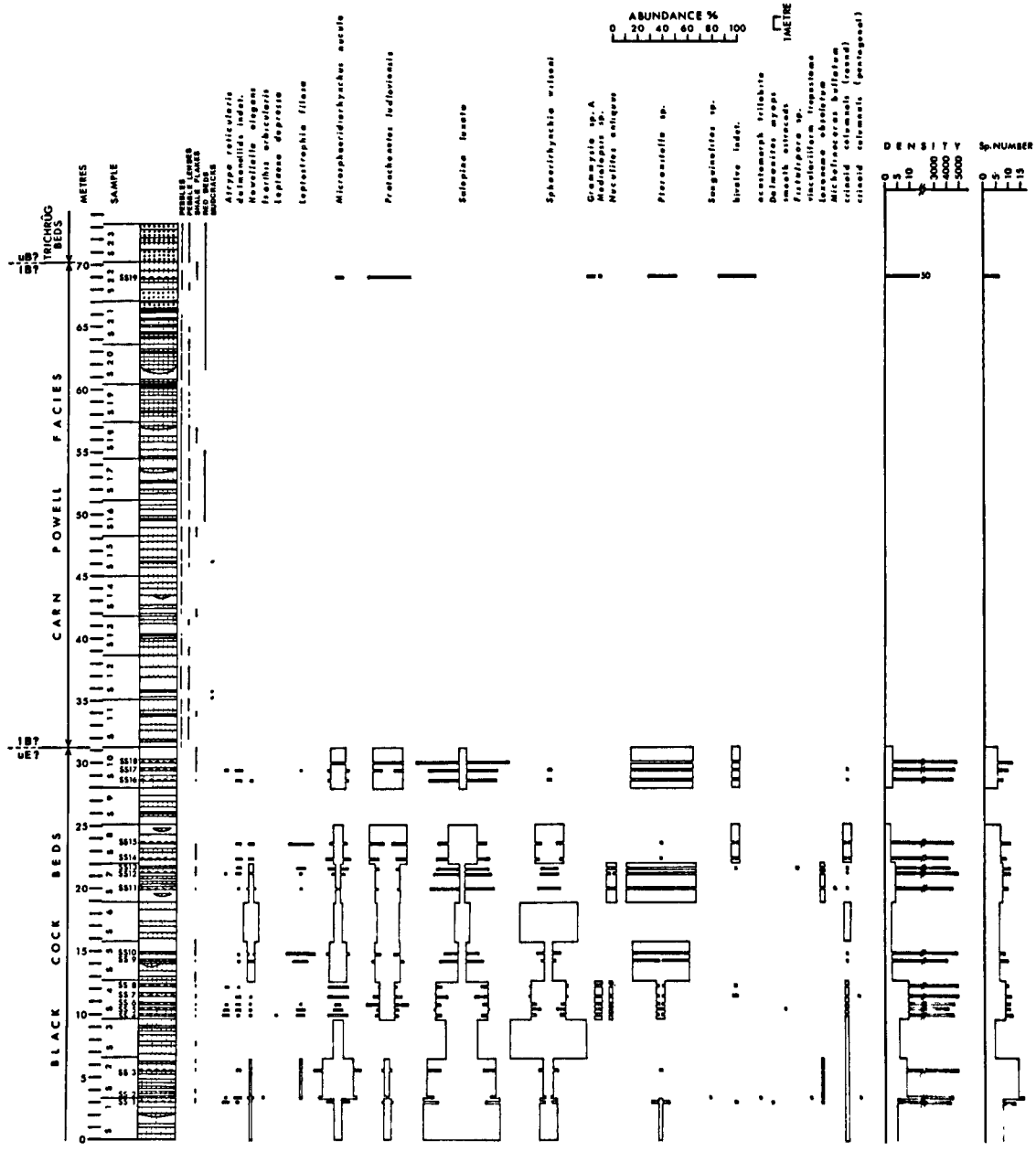


Fig. 5.4 The upper Eltonian and Bringewoodian succession and fauna in the Sawdde Valley

is taken at the base of sample S11 i.e. at the base of the lowest pebbly sandstone, below which the finer grained units are fossiliferous and above which they are not. At this level thick sandstones become dominant and thin interbedded shales and siltstones become rare. Most of these sandstones are pebbly, red beds occur near the top of the succession. The sandstones often show trough and tabular cross bedding, basal pebble beds or basal intraformational conglomerates of mud flakes. Channels are present in the sequence.

These strata are virtually unfossiliferous, with the only fossils present occurring in an intraformational basal lag conglomerate of shale chips (SS19); a few, rare, crinoid ossicles occur amongst the basal lag conglomerates of other sandstones.

The base of the unfossiliferous Trichrûg Beds was taken, as Potter (1960) defined it, where massive, red coloured, quartzitic pebbly sandstones and conglomerates become abundant; the base is therefore taken at the base of sample S23. The present author therefore records the Carn Powell Facies as 38.88 m thick, which compares well with Potter & Price's (1965) estimate of 41.12 m (135 feet). As discussed previously (p.136,137) it is possible that the Carn Powell Facies is of lower Bringewoodian age.

iii) Cennen

The section examined in the valley of the Afon Cennen was a road cutting on the western side of the A476, some 4 km south-south-west of Llandeilo. This section has been described by Potter (1960), Potter & Price (1965) and Squirrell & White (1978). In this area the uppermost strata of the Black Cock Beds which Potter (1960) and Potter & Price (1965) regarded as the lateral equivalents of the Carn Powell Facies were renamed the Grammysia Beds by Squirrell & White (1978) who also renamed the rest of Potter & Price's Black Cock Beds the Coed Wenallt Beds. The underlying Lletty Bed Facies of Potter & Price was renamed the Lletty Beds by Squirrell & White. The terminology of Squirrell & White is used in this chapter for Ludlovian strata in the Cennen Valley. The results of the present author's investigation of the section are summarised in Fig. 5.5.

The examined section commenced at SN 60991918 in the upper part of the Coed Wenallt Beds. This unit consists of a series of micaceous, bluish to greenish grey, irregularly and thickly flaggy siltstones (units 1 to 5 cm thick) with ripple cross bedding, mud draped ripples and extensive bioturbation. Interbedded with these strata are thin mudstones, shales

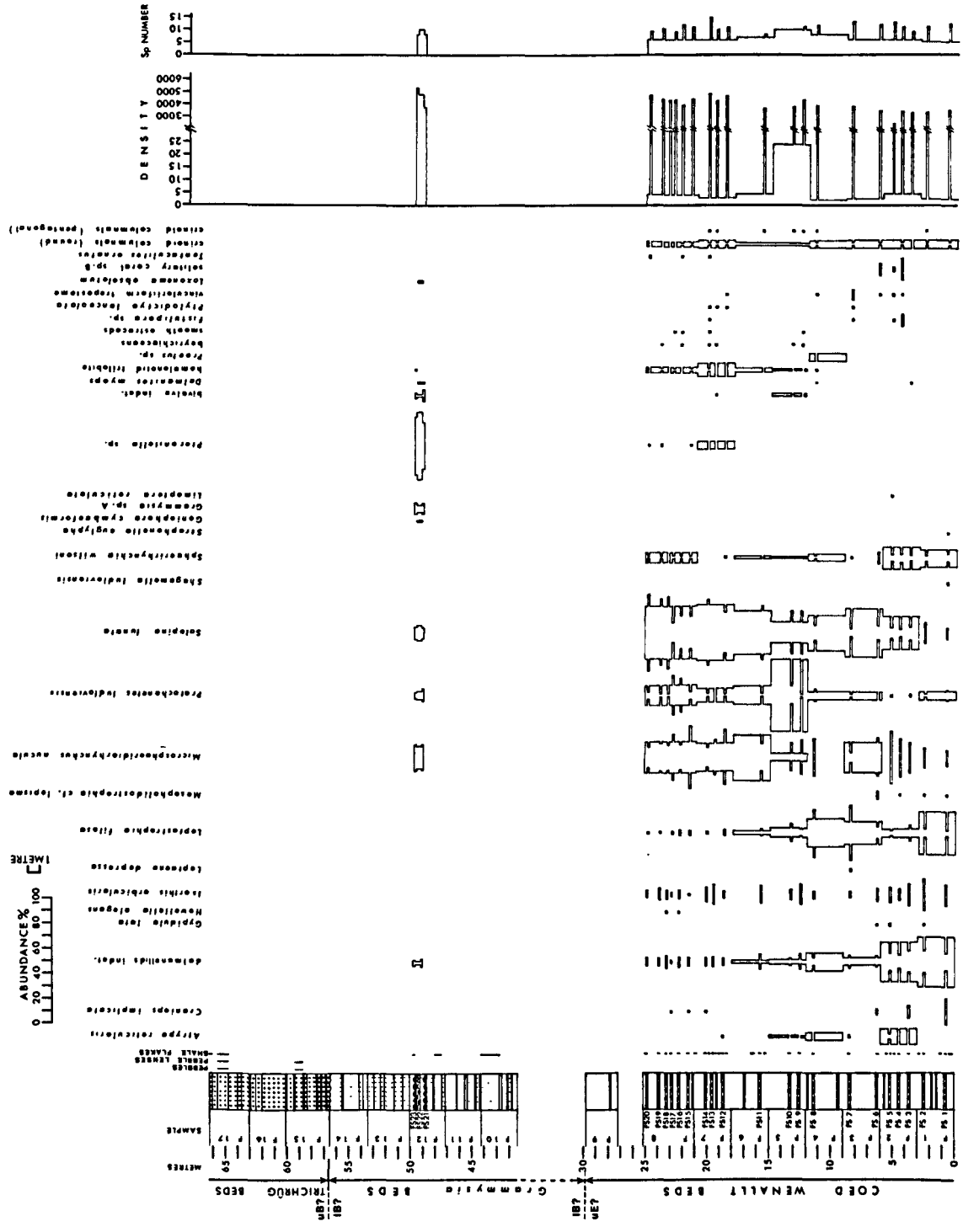


Fig. 5.5 The upper Eltonian and Bringewoodian succession and fauna in the Cennen Valley

and shell beds. A sparse fauna occurs sporadically in the strata between the shell beds. M. nucula, S. lunata and P. ludloviensis dominate the fauna.

The junction of the Coed Wenallt Beds with the overlying Grammysia Beds is not seen in this section, as a gap in exposure of 11.55 m follows the uppermost visible Coed Wenallt Beds. However, contrary to the claim by Squirrell & White (1978, p.13) that the uppermost Grammysia Beds are not exposed in this section a continuous thickness of 15.27 m was measured below the basal Trichrug Beds which overly them. It is puzzling that Squirrell & White (1978, Plate 2a, p.13) regarded these strata (the first 15.27 m of beds above the gap noted above) as Trichrûg Beds since this series of greenish grey, thick, fine to medium grained (but not pebbly) sandstones with interbedded siltstones and shales is identical to the description of the Grammysia Beds given by Squirrell & White (1978, p.11), Potter & Price (1965) and Potter (1960) but is dissimilar from the description of the Trichrûg Beds of this area given by all the above authors, who record the latter unit as being lighter in colour (creamish grey), coarser in texture (coarse grained sandstones with pebbly units) and with only minor, thin, finer interbedded units. The discovery by this author of 3 shell beds (FS21 to FS23) in these finer grained sandstones, beneath strata of typical Trichrûg Bed lithology as described above, and the presence of sporadic crinoid ossicles throughout these beds confirms that they belong to the Grammysia Beds and not the Trichrûg Beds, since the latter are acknowledged to be unfossiliferous by all the above authors. The shell beds contain abundant Pteronitella sp.

As noted above, the Trichrûg Beds and Grammysia Beds are markedly different and the junction between them can be placed at the base of sample F15 where unfossiliferous lighter coloured, coarser, occasionally pebbly sandstones, with thin and rare shale interbeds, succeed the darker coloured, finer, non pebbly, fossiliferous sandstones of the Grammysia Beds. As Squirrell & White (1978, p.12-13) note from other sections they examined, the junction is sharp and irregular; they suggested a hiatus in sedimentation to explain this break. The lowermost 9.67 m of the Trichrûg Beds were examined and collected i.e. up to a horizon at SN 61001911.

When Potter (1960) visited this section the basal junction of the Grammysia Beds could be located to within 0.6 m since what are now called Coed Wenallt Beds and Grammysia Beds could be seen either side of a 0.6 m gap in exposure. The upper junction of the Grammysia Beds (with

the Trichrûg Beds) was also exposed and therefore Potter (1960) was able to accurately measure the thickness of the Grammysia Beds in this section as 28.35 m (93 feet). If this thickness is measured from the upper junction of the Grammysia Beds as identified in this study (which from Potter's (1960) description of this section is where he took it too) then the base of the Grammysia Beds should lie 1.53 m below the highest Coed Wenallt Beds now visible in the section. These latter strata, although they are unfossiliferous, are however undoubtedly Coed Wenallt Beds on lithological grounds. However the small difference in the thickness of the Grammysia Beds (28.35 m) as measured by Potter (1960) and the combined thickness of the upper Grammysia Beds, as exposed today in the section, plus the thickness of unexposed strata above the last exposure of the Coed Wenallt Beds (a total of 26.82 m) strongly suggests that the base of the Grammysia Beds must be extremely close to the top of the Coed Wenallt Beds seen in the section at present. Therefore the boundary is placed at the level of the topmost Coed Wenallt Beds exposed i.e. at the top of sample F9. The unfossiliferous nature of these uppermost Coed Wenallt Beds probably reflects their proximity to the largely unfossiliferous Grammysia Beds overlying them.

Assuming the above arguments are correct the uppermost 29.8 m of the Coed Wenallt Beds were examined during this study and the Grammysia Beds are recorded as being 26.82 m thick (at a maximum). As discussed previously (p.136,137) it is possible that the Grammysia Beds are lower Bringewoodian in age.

SEDIMENTOLOGY

In order to successfully interpret the distribution pattern and abundance of fossil organisms in the strata of this region it is necessary to have a knowledge of the depositional environments of the time. The latter was obtained from sedimentological investigations in which the environmental interpretations of previous authors was refined and updated. Detailed petrographic work was not carried out but about 10 thin sections and about 50 polished sawn cut blocks of each lithology were examined. Considering the uncertainty of correlation between the rocks of this area and the type section at Ludlow (p. 136) it was considered necessary to collect and examine rocks both above and below what are here considered strata of likely lower Bringewoodian age (Fig. 5.1) in the 3 examined sections. This was in case, at some future date, rocks above or below

this latter level turn out to in fact be lower Bringewoodian in age and because a knowledge of the depositional environments of these strata allows the rocks suggested here as lower Bringewoodian in age to be considered in context.

Note

The angularity of the non pebble grains in all these rocks is very marked and could be interpreted as a result of rapid erosion, transport and deposition of material; this would be true of some of the deposits (e.g. the alluvial deposits) but in others (e.g. the outer delta platform) such an interpretation would be contrary to other evidence (e.g. the extensive bioturbation of the latter sediments, which suggests slow deposition, probably out of suspension). Recently, however, Potter (1977) has shown that in the strongly compacted rocks of the Trichrûg Beds the sand sized grains, as opposed to the pebble sized ones, are more angular than the latter, purely as a result of pressure solution and concurrent crystallisation of dissolved silica in the adjacent pore spaces. Potter (1977) suggests that these processes take place in all strongly compacted sediments to effectively change the size and shape of the grains in the rock. The marked angularity of the clastic grains in the rocks of the Llandovery-Llandeilo area can therefore be explained by the strong compaction they have undergone. Grain angularity was not therefore used as a diagnostic factor for interpreting the environments of deposition.

Gwydderig - upper Black Cock Beds

These strata consist of bluish to greenish grey, irregularly and thickly flaggy (2 to 5 cm thick) siltstones. Most of the sediments are horizontally or current ripple cross laminated (Plate 4, Fig. 2). These laminae are usually 1 to 2 mm thick and the lighter laminae are siltier. Numerous tracks, trails and burrows are present and occasionally almost all the sedimentary structures of a bed may be destroyed by intensive mottling (Plate 4, Fig. 1). Muscovite mica is common on many bedding planes. The fauna is mostly found disarticulated but unfragmented in numerous small patches and thin lenses (about 1 cm thick and 10 cm across) as well as occurring, less commonly, scattered throughout the sediment. The faunal composition of these scattered sporadic fossils and those of the small patches is identical and they were recorded together as disturbed neighbourhood assemblages (Scott 1974) i.e. they have probably been disturbed from their life position by burrowers, predators, gravity or weak currents but have not been moved far. Occasional shell

EXPLANATION OF PLATE 4

Sediments Of The Llandovery-Llandeilo Area

Fig. 1 Bioturbated siltstone, mottling due to extensive bioturbation (x 1); upper Black Cock Beds, Gwydderig. Sample G6.

Fig. 2 Laminated and ripple cross laminated siltstones overlying a layer of bioclasts, interpreted as a storm deposit (x 3/4); upper Black Cock Beds, Gwydderig. Sample G7, shell bed is GS4.

Fig. 3 Wave rippled upper surface of thin sandstone unit; upper Black Cock Beds, Sawdde.

Fig. 4 Interference wave rippled upper surfaces of thin sandstone units; upper Black Cock Beds, Sawdde.

Fig. 5 Mud draped rippled sandstone showing two opposite directions of ripple cross lamination and a reactivation surface (x 1.1/4); upper Black Cock Beds, Sawdde. Sample S7.

Fig. 6 Lenticular bedded siltstone with mudstone (x 1), cf. Reineck & Wunderlich (1968); upper Black Cock Beds, Sawdde. Sample S6.

Fig. 7 Laminated sandstone unit showing pebbly base (x 3/4); Carn Powell Facies, Sawdde. Sample S14.

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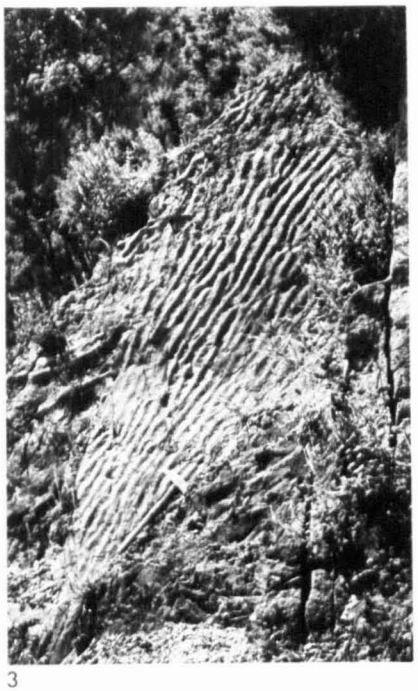

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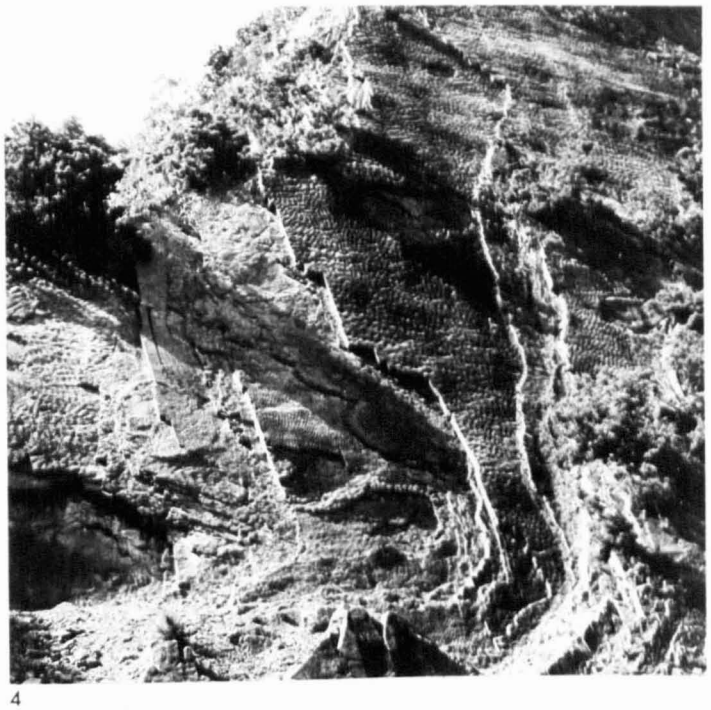

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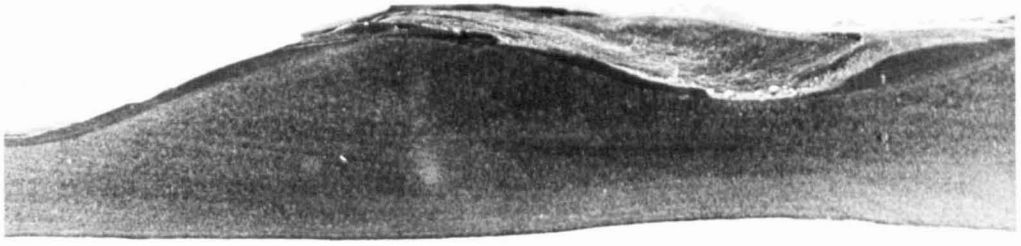

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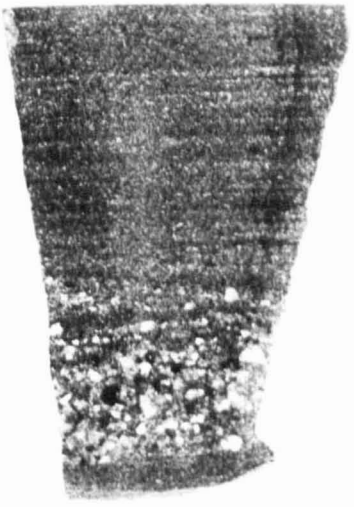

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PLATE 4

beds also occur, they are sharp, erosively, based units packed with mostly fragmented and disarticulated fossils, together with some mudclasts. The faunal assemblages of these shell beds were recorded as transported assemblages (Scott 1974) i.e. they have accumulated totally by sedimentological processes. These shell beds are either overlain by laminated sediments (Plate 4, Fig. 2) or grade up into the succeeding deposits. The upper layers of these units may be extensively burrowed. The shell beds average 6 cm thick (range 3 to 8 cm). Sharp, erosively based, sandstone units which average 6 cm thick (range 4 to 12 cm) are also recorded from these strata. These sandstones are medium to fine grained, unfossiliferous and are parallel laminated, cross laminated or graded.

In thin section the siltstones consist mostly of moderately well sorted, silt sized, equidimensional quartz which is mostly subangular but varies from angular to subrounded. Muscovite mica is not uncommon and angular plagioclase grains are present. Laminations arise from layers richer in quartz grains. These minerals are set in a dominantly chloritic clay matrix which separates the individual clastic grains. The sandstones show an abundance of quite well sorted fine sand grade quartz which is mostly subangular to subrounded, micas are also present. These minerals are set in a clay matrix. Laminations are formed by layers richer in quartz.

Interpretation. Previous authors considered that these deposits represented relatively shallow marine shelf environments (p. 137). However, it is possible to be more specific and assign them to an outer delta platform or inner prodelta environment. Such sediments as those described above are typical of this environment. The laminations arise both from variations in sediment supply (e.g. river discharge) and reworking of material by currents, which also produced ripple cross lamination. Sediments in this environment are usually quite extensively bioturbated, producing mottled sediment, since sedimentation was slow enough to allow fairly extensive bioturbation, although not generally so slow that all the primary sedimentary structures are destroyed (Moore & Scrutton 1957). The frequent disarticulation of the shells and their concentration into small patches indicates a moderately turbulent environment. The shell beds show all the features of proximal storm deposits (as discussed on p.64-67). Such storm deposits are typical of this environment (Bowen et al. 1974). The sandstone units represent discrete incursions of sediment laden currents into this environment, and are directly comparable

with the river generated turbidites of Collinson (1970); which have been recorded from a similar setting to that inferred here in the upper Carboniferous of Devon (Elliott 1976).

Sediments identical to those described above are known from outer delta platform and inner prodelta environments both in modern settings (e.g. Allen (1964, 1965, 1970) from the Niger Delta, Donaldson et al. (1970) from the Guadalupe Delta of Texas and Fisk et al. (1954) and Moore & Scrutton (1957) from the Mississippi Delta) and ancient settings (e.g. the Upper Devonian Sonyea Group of New York (Sutton et al. 1970)).

Gwydderig - lower Lower Cwm Clŷd Beds

These beds consist of blue grey, irregularly flaggy (1 to 4 cm thick), coarse siltstones and fine sandstones. Most of these strata are either parallel or ripple cross laminated; the laminae are mostly about 1 to 2 mm thick with the lighter laminae appearing siltier. Bioturbation of these deposits is extensive and many beds have only traces of their original primary structures left. Muscovite is common on bedding planes. As in the underlying strata the fauna is found both scattered through the sediment and as small patches of similar faunal composition (i.e. disturbed neighbourhood assemblages). Thin seams of well rounded quartz granules, 2 to 4 mm in diameter, are also present, as are scours up to 6 cm wide.

In thin section equidimensional subrounded and particularly angular quartz grains dominate, with minor constituents of plagioclase quartzite rock fragments and muscovite set in a dominantly chloritic clay matrix. Laminations are due to layers richer in quartz grains. The granules are of either quartz or quartzite rock fragments.

Interpretation. The similarity of this lithological facies to the underlying one suggests a similar environment, although the coarser grain size, the granule lenses and the presence of scours, together with the lack of river generated turbidites suggests nearer shore, higher energy environment, further onto the delta platform, in which reworking of the sediments may have been more extensive.

Sawdde - upper Black Cock Beds

These strata consist of an alternation of dark blue grey, thick units (greater than 20 cm) of medium grained sandstone with greenish grey and blue grey siltstones, mudstones and thin (less than 10 cm) fine grained sandstone units. The mudstones and siltstones often show lenticular bedding (Plate 4, Fig. 6). The thin sandstone beds are often wedge shaped

and have sharp erosional bases, their tops often show superbly preserved mud draped wave and interference wave ripples (Plate 4, Figs. 3, 4). In section these units may show parallel or ripple cross lamination; in some cases herringbone cross bedding is seen and reactivation surfaces are common (Plate 4, Fig. 5). The surfaces of the ripples are often covered with up to 6 different types of trails and several kinds of burrows. Shale fragments may be found in the siltstones, mudstones and thin sandstones and their bedding surfaces are commonly covered with abundant muscovite mica and also, but more rarely, biotite and plant fragments. Ball and pillow structures and scoured surfaces were also seen in these sediments and bioturbation is quite common. Interbedded with the siltstones, mudstones and thin sandstones are shell beds (4 to 10 cm thick) with sharp, erosive, bases; most of the fauna is broken and disarticulated and shale clasts are common. The fauna of the shell beds was recorded as a transported assemblage. These shell beds grade upwards into medium grained sandstone and finally siltstone; occasionally the succeeding sediment is laminated.

In thin section the siltstones are moderately well sorted, consisting mostly of silt sized, angular to subrounded but mainly subangular quartz grains, with plagioclase and muscovite as minor constituents. These clastic grains are set in a dominantly chloritic clay matrix; grains are matrix supported. The laminations arise from more quartz rich layers. The fine grained sandstones have a grain supported texture and consist mostly of well sorted angular to subangular quartz grains with minor amounts of plagioclase, muscovite and rock fragments of quartzitic sandstone (all of fine sand grade) in a dominantly chloritic clay matrix.

The thick bedded sandstones may be wedge shaped and have sharp erosional bases. At first they appear massive. However, on closer examination many can be seen to show parallel lamination, cross bedding, and they may be graded, sometimes with shells or shale flakes at their bases emphasising the grading. Grooves and structures which resemble flutes are rarely seen on the bases of these sandstones. The shells found in the base of these sandstones are often broken and disarticulated, they are regarded as transported assemblages.

In thin section these thick sandstones are seen to consist mostly of moderately well sorted, fine to medium grained, angular to subangular quartz grains, with minor amounts of plagioclase and muscovite in a clay matrix; the texture is grain supported. Laminations arise from layers richer in quartz.

Occasional channels, up to 0.2 m deep and up to 2 m wide, may be found in all the above sediments; they are generally filled with ripple cross laminated or parallel laminated sandstones. The lowest sandstones of these channels often have basal shale fragments.

The fauna of these upper Black Cock Beds which is found outside the various shell beds is extremely sparse, it occurs sporadically throughout the siltstones, mudstones, thin sandstones and the top surfaces of the thick sandstones. These faunas show all the features of the disturbed neighbourhood assemblages of Scott (1974).

Interpretation. The laminated or lenticular bedded mudstones, siltstones and thin fine sandstones, which contain abundant mud draped wave and interference wave ripples (some with evidence of bidirectionally orientated current systems) reactivation surfaces and intraformational mudflake conglomerates are typical of very shallow water, subtidal or intertidal, conditions (e.g. McKee 1957; Evans 1965; Thompson 1968; Howard & Reineck 1972; Reineck & Singh 1973; de Raaf et al. 1977; Rust 1977; Johnson 1978). The shell beds interbedded with these sediments show all the features of proximal storm beds (p.64-67). Howard & Reineck (1972) have interpreted similar shell beds from a very shallow water nearshore environment as being storm produced. Interbedded with these shallow water sediments are occasional discrete, thick, sandstone bodies, which may have a fauna at their base and or shale clasts.

The position of these deposits in the succession, the scale of the sedimentary structure within them and the overall deltaic setting suggests that these strata were deposited in an interdistributary bay. Such bays are generally very shallow, with water less than 3 or 4 m deep (Coleman et al. 1964; Elliott 1974) which in many cases pass shorewards into tidal flats (Morgan 1970). Much of the sediment of such bays is derived from overbank flooding of the distributaries during a single flood, when sediment laden waters spill over the channel walls as sheet flow and fine grained sediment is deposited over the entire bay. Waves and tides then rework this sediment to produce a finely laminated or lenticular bedded deposit of muds and silts which may be rippled; although subsequent bioturbation may destroy some of these primary features (Coleman et al. 1964; Elliott 1974) it never destroys them all. This implies quite high rates of sedimentation or the rarity of burrowing species (Moore & Scrutton 1957).

In such modern environments these fine grained sediments alternate with discrete erosively based sandstone beds, some of which may

wedge out. The latter have been shown to arise from levee deposits (Allen 1965) and crevasse splay sands (Arndorfer 1973). The former are produced by the coarser material of overbank sheet flows settling out on the bay margins and therefore contributing to levee development (Elliott 1974). Since these levees become finer away from the channel margin, encroachment of the levees into the bays produces an alternation of coarse and fine beds (Elliott 1974). Allen (1965), recording such beds from the modern Niger Delta, noted the coarse beds had parallel or current ripple lamination, erosive bases and graded up into the finer overlying beds. The coarser beds of interdistributary bays can also result from crevasse splay deposits. These result from flood waters cutting small crevasse channels in the levee crest resulting in a sudden discrete incursion of sediment laden flood waters into a limited area of the bay (Arndorfer 1973). Often the sediment is transported as a density flow (Elliott 1974, 1975). Such lobes of sediment extend across the lower parts of the levee (therefore contributing to levee development (Arndorfer 1973)) and beyond, finally wedging out into the bay. The thickness of the deposit and its sedimentary structures depend on the characteristics of the flow and the magnitude of the flood, but units 1 to 2 m thick result from a fairly large scale flood (Elliott 1974). These crevasse splays occur as discrete coarse beds amongst bay mud and silt (Elliott 1974). These crevasse splay sands may contain flutes and grooves on their erosive bases indicating sheet erosion and they often show many features of turbidite beds (such as grading, parallel lamination and cross lamination) indicating deposition from a waning flow (Stanley 1968; Collinson 1969; Elliott 1974). Minor channels are also present in modern interdistributary bays, they may be crevasse channels extending from the distributary into the bay (Fisk *et al.* 1954; Coleman *et al.* 1964) or tidal channels as described from the modern Niger Delta (Oomkins 1974). Both kinds are filled with current ripple laminated and parallel laminated sandstones whose bases may have shale chip inclusions.

The finer sediments of the Sawdde upper Black Cock Beds are therefore similar to those deposited in modern interdistributary bays. While the sandstones are comparable with modern examples of levee and crevasse splay deposits into such bays. The shale fragments and shells found in the bases of some of the thick sandstone beds indicate erosion of the underlying sediment and the suspension and possibly large scale transport and sorting of shells.

The whole succession as well as being identical to modern

interdistributary bays being filled by crevasse splay sands and levee deposits is also similar to such environments interpreted from the geological column. Examples of these are the Upper Carboniferous of the northern Pennines (Elliott 1975) and the Upper Carboniferous of the central Pennines (Collinson 1969).

Other environments may produce similar sequences to those of interdistributary bays e.g. flood plains (Allen 1965) or the 'channel fill sequences' of the Rhône Delta (Oomkins 1967, 1970) which Elliott (1974) interpreted as crevasse splays and minor mouth bars forming in coastal lakes and lagoons. However the presence of shells, regarded as marine, in the Sawdde section suggests that an interdistributary bay environment was the most likely setting (cf. Elliott 1974).

Potter's (1960) suggestion that these deposits represented deposition in very shallow water near the mouth of a river is therefore upheld but modified in detail. In this environment sedimentation rates were variable; the sediment was frequently reworked and waves and currents were probably quite strong; salinity was probably low and variable due to river discharge.

Sawdde - Carn Powell Facies

These strata also consist of an alternation of thick sandstones with thin shales and siltstones. However thick pebbly sandstones now make up virtually the complete thickness of these beds, with only very thin shales and siltstones between them. Near the top of the sequence many of the beds are red in colour and a few very coarse grained sandstones occur.

The pebbly sandstones are medium grained, sharp based and may be either purplish red or dark blue grey in colour. Pebbles are up to 2 cm in diameter but more generally are 0.5 to 1 cm in diameter. In hand specimen most of the pebbles are well rounded and of quartz and quartzitic sandstone, although, angular, tabular orthoclase crystals may be found and may form up to 50% of the pebbles in some units. Shale chips may also be found in these rocks. These sandstones often show tabular and trough cross bedding and their bases often contain many pebbles (Plate 4, Fig. 7), or shale fragments if they overly shales. The bedding surface of these sandstones is flat and commonly shows primary current lineation. The upper surfaces of these sandstones may be cut by channels (2 to 10 m wide and up to 0.46 m deep) whose bases contain pebbles and whose fill is one of parallel and cross bedded sandstone.

In thin section the pebbles of these sandstones are seen to consist of mainly well rounded quartzitic sandstone and quartz together with less common siltstone and a fine grained quartz and feldspar igneous rock; orthoclase clasts are angular and heavily altered. The sand grade is composed of a tightly packed equigranular mosaic of moderately sorted, angular to subangular, medium sand sized quartz grains and a few rare plagioclase and orthoclase grains; micas are rare. Many of the boundaries between the grains are sutured, the clay matrix is confined to the spaces between some of the grains.

The coarse sandstones are always purple red in colour. They are similar to the sandstones described above, except that they are coarser (coarse sand grade), pebbles are larger (up to 4 cm in diameter) and feldspar pebbles are commoner.

Interbedded with the sandstones are blue grey or pinkish shales and thinly flaggy siltstones which have abundant flakes of muscovite mica scattered over their bedding surfaces. Ripple cross bedding is common, bioturbation rare and mudcracks occur sporadically.

Apart from the odd crinoid ossicle found in the basal pebbly layer of some sandstones the only fauna found in these beds is a number of fossils in the base of a pebbly sandstone (SS19). Here they occur broken, disarticulated and scattered between brownish red shale fragments, they were recorded as a transported assemblage.

Interpretation. Potter (1960) considered that these sediments were deposited on a broad flat subaerial deltaic or alluvial plain, fairly close to the area of provenance. High tides were thought to have advanced over this plain, explaining the presence of rill marks and sedimentary structures which indicate flow directions opposite to the vast majority. Reineck & Singh (1973) note however that rill marks may be found on river banks and flood plains, following a flood period, as well as in the intertidal zone.

This sequence of coarse often pebbly, graded, tabular or trough bedded, erosively based sandstones, whose upper surfaces may be channelled and whose bases often have basal lag conglomerates, and interbedded siltstones and mudstones, which may show mudcracks - indicating periodic exposure - is interpreted as one of channel and overbank deposits. The lower eroded surfaces of the sandstones indicate lateral migration of a channel into an area of previously overbank deposition. The fine members probably represent the overbank deposition of many channels and channel

belts with different courses across what was probably a coastal plain. The channels or channel belts may have been either simple or braided. The predominance of sandstones often with little or no fine sediment between them suggests deposition by rivers of low sinuosity whose channels could wander freely from side to side. An environment in which braided streams were unrestricted in their lateral wandering is therefore suggested (cf. Allen & Friend 1968). The high rate of channel migration may have been due to the absence of plant growth stabilising the channel margins (McCave 1968). Some of the thinner sandstones are probably too thin to represent channel deposits and may therefore possibly represent crevasse splay or levee deposition. As Potter (1960) suggests the primary red colour of many of these strata suggest a subaerial environment of deposition. The presence of large angular orthoclase feldspars agrees with Potter's (1960) conclusions from heavy mineral analyses, that these sediments were subjected to rapid erosion, transport and deposition.

The bimodality of currents noted by Potter (1960), the presence of marine shells in the long conglomerate of shale chips, in one of the sandstones,and the presence of crinoid ossicles in the base of many others suggests that these channels were at times influenced by tidal waters (Coleman et al. 1964; Sutton et al. 1970). The environment was therefore dominantly alluvial with some tidal influence, salinities were probably low and variable and exposure would have been high.

Such tidally influenced nearshore distributary channels are seen at various localities today, e.g. the Niger Delta, Mississippi Delta and Rhône Delta, and produce similar sequences to the one described above (Allen 1964, 1965, 1970; Coleman et al. 1964; Oomkins 1967, 1970, 1974). Similar sequences are also known from ancient deposits interpreted as representing such environments e.g. Allen & Friend (1968), McCave (1968) and Sutton et al. (1970) from the Devonian of New York and Collinson (1969) and Elliott (1975, 1976) from the Upper Carboniferous of Britain. In all these cases such deposits are closely associated with (i.e. they pass laterally into or overly) shallow water tidally influenced, often interdistributary environments and are therefore analogous to the Sawdde section since the upper Black Cock Beds beneath are interpreted as tidally influenced interdistributary bay deposits.

Sawdde - lower Trichrûg Beds

These strata were not examined in detail as only the basal 3 m are exposed in the section examined. The beds seen are reddish purple

pebbly coarse grained sandstones and rarer pebbly, medium grained, sandstones. They appear to be identical to the pebbly sandstones and coarse sandstones of the Carn Powell Facies described above except that they are totally unfossiliferous and with the pebbly lithology now dominating.

Interpretation. Potter (1960, 1968, 1977) considered that these beds had been deposited by braided rivers on a deltaic plane under subaerial, strongly oxidising conditions.

Cennen - upper Coed Wenallt Beds

These beds consist of a series of bluish to greenish grey irregular and thickly flaggy (1 to 5 cm thick) coarse siltstones with rarer interbedded thin shaly mudstone units (3 to 10 cm thick) and shell beds (5 to 10 cm thick). The siltstones are parallel laminated or ripple cross laminated with mud drapes over the ripples, some of which appear to be wave ripples, although these primary structures may be virtually destroyed by burrows and bioturbation at some levels. Scours up to 4 cm wide were seen on some bedding planes. Muscovite mica is commonly scattered on bedding planes, which often show tracks and trails. Faunal remains are found rarely and sporadically outside the shell beds and also occasionally as small patches, in either case shells are often disarticulated but not fragmented; they were recorded as disturbed neighbourhood assemblages. In the shell beds, fossils are mostly disarticulated and fragmented, mudclasts are found, and they are overlain by laminated sand or grade up into the succeeding beds; their upper surfaces may be extensively bioturbated. The fauna of the shell beds were recorded as transported assemblages.

In thin section the siltstones are seen to consist of silt grade quite well sorted, equidimensional, subangular to subrounded, but mostly subangular quartz together with minor amounts of muscovite and angular plagioclase in a clay matrix; grains are matrix supported. The laminations arise from layers richer in quartz grains.

Interpretation. Potter (1960) considered these deposits to be of shallow marine shelf origin. However, it is possible to be more specific. Although they are similar in appearance to the Lower Cwm Clŷd Beds of the Gwydderig (except that they lack the lenses of granules) the presence of mud drapes on the ripples, some of which are of wave origin, suggests that they formed further inshore on the delta platform, probably in quite shallow water. The fact that bioturbation never destroys all the sedimentary structures in any one bed suggests quite high rates of deposition

or a rarity of burrowing forms (Moore & Scrutton 1957). Salinities may have been low and variable this far onto the delta platform and wave buffeting was possibly quite strong.

Cennen - Grammysia Beds

These strata consist of thick (mostly greater than 40 cm) medium grained sandstone beds which alternate with thinner (mostly less than 10 cm) units of shales and siltstones. The latter are identical to those of the Sawdde upper Black Cock Beds described above, i.e. they are laminated or lenticular bedded with mud draped wave ripples; tracks and trails occur on their surfaces and intraformational mudflake conglomerates are noted. The thick sandstones are also similar to those of the upper Black Cock Beds of the Sawdde. They are greenish grey, slightly wedge bedded and have sharp bases; at first they appear massive, but careful examination reveals parallel lamination, cross lamination and grading. The latter is sometimes emphasised by a basal shell layer from 5 to 15 cm thick.

In thin section the sandstones are seen to consist of moderately well sorted fine to medium sand sized particles. Quartz is dominant as angular and subangular grains while minor constituents are orthoclase, plagioclase and quartzitic sandstone; muscovite is rare. These clastic grains are set in a dominantly chloritic clay matrix. The siltstones are moderately well sorted and are dominantly composed of subangular quartz grains with minor amounts of plagioclase and muscovite set in a chloritic clay matrix; the grains are matrix supported. Laminations arise from more quartz rich layers.

The fauna of these rocks is restricted to the odd crinoid ossicle in some of the sediments and 3 shell layers from 5 to 15 cm thick in the base of sandstones near the top of the sequence. Many of the shells are broken and there are many shell fragments in the rock, they are obviously transported assemblages.

Interpretation. The similarity of this sequence to that of the Sawdde upper Black Cock Beds strongly suggests a similar environment of deposition. These beds are therefore considered to have formed in an interdistributary bay in which sedimentation was quite high and variable, reworking common, buffeting by waves extensive and salinities variable. In this bay crevasse splays and levee deposits accumulated. This is therefore a refinement on Potter's (1960) vague conclusion that these strata are of shallow marine shelf origin.

Cennen - lower Trichrûg Beds

These totally unfossiliferous rocks were not examined in detail.

They consist of a series of thick very coarse grained cream coloured, mostly pebbly, sandstones and rare thin seams of interbedded creamish grey or greenish grey shales. The sandstones have pebbles scattered throughout them and as lenses and stringers. These pebbles are of well rounded quartz and quartzitic sandstone up to 4 cm across, but more usually 1 cm in diameter; some angular feldspars are often seen and may be locally quite common. Pebble lenses at the base of these sandstone units, or shale fragments, if they overly a shale are quite common.

Seen in thin section the pebbles are mostly of quartzitic sandstone with rarer quartz, highly altered orthoclase, plagioclase and a fine grained igneous rock. The coarse sand grade is of poorly sorted angular and subangular quartz grains, together with less common orthoclase feldspar and rare microcline, plagioclase and quartzitic with an interstitial clay matrix. Many of the quartz boundaries are sutured.

Interpretation. Potter (1960) and Potter & Price (1965) interpreted these sediments as alluvial deposits forming near the area of provenance on the alluvial plain. Such an interpretation is likely from Potter's (1960) sedimentological studies but does imply a rapid progradation of the delta and some erosion to explain the presence of this facies above one considered to have formed in an interdistributary bay. In fact both this author and Squirrell & White (1978, p.12-13) record a sharp, irregular contact between the Grammysia Beds and the Trichrûg Beds; Squirrell & White considered this sharp junction to represent a hiatus in sedimentation. It is here considered more likely that this junction represents erosion of the transitional deposits between two environments.

Conclusions Of Sedimentological Investigations

Assuming the correlations with the type area at Ludlow (Fig. 5.1) are correct, we can summarise the above work as follows.

upper Eltonian. In the Gwydderig area a moderately turbulent, outer deltaic platform or inner prodelta environment existed where sedimentation was quite slow and reworking persistent. In this area river generated turbidites and storm deposits also accumulated. Further southwest in the Sawdde region a very shallow water interdistributary bay existed, in which sedimentation rates were variable, reworking of the deposits by waves was common and buffeting by waves and currents was probably quite extensive; the proximity of distributaries implies low and variable salinities here. This bay was slowly being filled with overbank,

levee and crevasse splay sands which occasionally have basal shale chip and or shell layers indicating erosion of the underlying sediment. Interbedded layers of shells were produced by storms. Crevasse or tidal channels cut through these deposits. Still further south-west in the Cennen area a shallow water, quite high energy, inshore deltaic platform environment existed; wave influence, storm transport of shells and possibly low and variable salinities are all environmental influences which can be inferred.

lower Bringewoodian. Although the environment was unchanged from the upper Eltonian in the Gwydderig region the effects of progradation of the delta are seen further south-west. In the Sawdde region the interdistributary bay had passed up into an area of subaerialy exposed tidally influenced distributary channels which often changed their courses and into which shells were rarely swept by tides or storms. To the sides of the channels overbank, levee and crevasse splay deposits accumulated. This environment appears to be dominantly alluvial, but with some tidal influence. Salinities were probably low and variable and exposure high. In the Cennen area the shallow nearshore deltaic platform environment had passed up into a very shallow water interdistributary bay in which sedimentation was quite high and reworking was common, buffeting by waves and currents was probably extensive and salinities low and variable. In this bay overbank, levee and crevasse splay deposits accumulated. The basal layers of shells and shale chips of these sandstones indicate erosion of the underlying sediment.

upper Bringewoodian. The effects of further delta progradation can now be seen in all sections. The Gwydderig region now lay well onto the delta platform, the environment was probably quite turbulent and reworking of the sediment more extensive than in the underlying environment. In the Sawdde district braided rivers deposited sediment on the delta plain in a subaerial, strongly oxidising environment; while in the Cennen region alluvial deposits accumulated near the area of provenance.

CONTINUOUS REGRESSION IN THE LUDLOVIAN?

The upper Eltonian to upper Bringewoodian deposits of the Llandovery-Llandeilo area were deposited in successively shallower environments, at each of the sections examined, it is therefore pertinent to consider whether continuous regression took place throughout the Ludlow in this area.

Calef & Hancock (1974) collected very widely spaced samples from

the Sawdde section between the basal Ludlow and the Trichrûg Beds. They assigned these collections to 'communities' for which they claimed depth significance. They implied (op. cit., p.799-801) that these 'communities' indicate continuous regression throughout the Ludlow in this and other areas, claiming (p.800) that they had found no evidence of widespread cyclical transgressions and regressions throughout the Ludlow as postulated by Phipps & Reeve (1967) for the Malverns. However, all that Calef & Hancock (1974) 'proved' was that there appears to have been a shallowing in water depth from the base of the Ludlow up to the Trichrûg Beds, something that previous workers in this area had long recognised (Price 1957; Potter 1960; Holland & Lawson 1963; Potter & Price 1965). What Calef & Hancock failed to realise (although it had been noted by the above authors) was that the largely alluvial Trichrûg Beds are overlain by marine Ludlovian rocks, clearly indicating the occurrence of a transgression late in the Ludlow.

McKerrow (1979) has recently reiterated the 'continuous regression through the Ludlovian' hypothesis for this area. However McKerrow (1979, Fig. 3) did not indicate the presence of Bringewoodian fluvial sediments in the Sawdde section but implies that they were deposited in moderately deep (Pentamerus 'ecogroup') water. From the above work this is obviously not so.

R. Marsh (1976) carried out chemical analyses of strata throughout the Ludlow Series a few kilometres north-east of the Gwydderig section, which he considered to indicate a cyclical series of transgressions and regressions, including a regression maximum in the Bringewoodian; this interpretation is identical to the scheme of regressions and transgressions proposed by Phipps & Reeve (1967) for the contemporary Malvern succession.

It is concluded that a continuous regression hypothesis for the Ludlovian of the Llandovery-Llandeilo area is untenable, as indeed it is for the Ludlovian of the shelf facies (p. 73).

FAUNA OF THE LLANDOVERY-LLANDEILO AREA

From the sandy facies of the Llandovery-Llandeilo region over 10,000 individual fossils, representing about 40 different species, were extracted during this study.

The comparison of faunas between sections examined in this area was aided by calculating mean relative abundances (see p.73 for method of calculation) for disturbed neighbourhood and transported assemblages from what are considered (Fig. 5.1) to be the equivalents of the upper Eltonian, lower Bringewoodian and upper Bringewoodian strata in them (Table 5.1).

Table 5.1 Mean relative abundance values for disturbed neighbourhood assemblages and transported assemblages (figures in brackets) in the upper Eltonian , lower Bringewoodian and upper Bringewoodian strata examined in the Gwydderig , Sawdde and Cennen sections

	UPPER ELTONIAN						LOWER BRINGEWOODIAN				UPPER BRINGEWOODIAN
	GWYDDERIG		SAWDDE		CENNEN		GWYDDERIG		SAWDDE	CENNEN	GWYDDERIG
A.reticularis	36.50	(49.93)		(1.19)	2.54	(0.36)	24.44	(47.93)			0.45
C.implicata						(1.89)					
dalmanellids indet.				(3.56)	12.46	(9.35)				(3.73)	
G.lata						(0.21)					
H.elegans	0.40		3.10	(2.19)		(0.04)	1.88				
I.clivosa	0.11					(0.05)					0.95
I.orbicularis	36.39	(24.43)		(0.03)		(10.94)	47.56	(36.03)			70.75
L.depressa	2.41	(0.93)		(0.01)		(0.14)	3.36				
L.filosa	13.89	(17.43)	0.22	(4.28)	11.38	(8.23)	3.78	(7.13)			3.75
M.cf.lepisma	0.06					(0.45)					
M.nucula	0.31		9.29	(15.19)	14.28	(25.76)	2.80	.	(6.80)	(19.93)	12.35
P.ludloviensis			15.23	(14.84)	15.41	(6.54)			(33.10)	(6.87)	
S.lunata			26.38	(41.50)	28.16	(27.39)				(10.47)	
S.ludloviensis						(0.14)					
S.wilsoni	2.31		20.89	(13.73)	6.56	(2.85)	10.88	(6.70)			10.40
S.euglypha	0.91	(1.03)				(0.04)	0.18				
G.cymbaeformis										(0.23)	
Grammysia sp. A									(5.40)	(7.33)	
L.reticulata						(0.14)					
Modiolopsis sp.			0.61						(2.70)		
N .antiquus			1.29	(0.04)							
Pteroniteila sp.			18.16	(1.36)	1.23	(0.14)			(23.00)	(44.90)	
Sanguinolites sp.				(0.03)							
bivalves indet.			1.56	(0.92)	0.18	(0.03)			(29.10)	(4.97)	
acastomorph trilobite				(0.06)							
D.myops	0.17			(0.07)		(0.11)	0.54				
homalonotid trilobite					1.93	(0.37)				(1.27)	
Proetus sp.					0.89						
beyrichiaceans						(0.32)					
smooth ostracods	0.14			(0.04)		(0.34)					
Fistulipora sp.	0.97	(0.63)		(0.05)		(0.75)	1.10				
P.lanceolata	0.37					(0.21)					
vinculariiform trepostome	4.14	(4.78)		(0.09)		(0.63)	2.64	(1.27)			
L.obsoletum			0.67	(0.13)						(0.37)	
solitary coral sp. B						(1.62)					
M.bullatum				(0.04)							
T.ornatus	0.14					(0.23)					
Tentaculites sp.											0.50
crinoid ossicles (round)	0.79	(0.90)	2.63	(0.56)	5.06	(0.57)	0.92	(0.93)			0.95
crinoid ossicles (pentagonal)				(0.07)		(0.23)					
TOTAL %	100.01	(100.06)	100.03	(99.98)	100.08	(100.07)	100.08	(99.99)	(100.10)	(100.07)	100.10
TOTAL NUMBER OF SPECIES	17	(8)	12	(23)	12	(30)	12	(6)	(6)	(10)	8
NUMBER OF SAMPLES	7	(4)	9	(18)	8	(20)	5	(3)	(1)	(3)	2
AVERAGE DENSITY	49.6	(740.8)	4.7	(4437.4)	5.9	(3985.7)	36.2	(768.7)	(50.0)	(4681.9)	18.4
AVERAGE SP. PER COLLECTION	10.0	(5.0)	6.3	(9.8)	6.8	(10.8)	10.2	(5.3)	(6.0)	(8.7)	7.0
AVERAGE SP. PER 100 INDIV.	9.3	(4.9)	-	(8.4)	9.1	(9.6)	9.9	(5.3)	(6.0)	(8.5)	6.9

By examining the lateral changes in the fauna within and between the local representatives of these Ludlovian divisions, as seen in Table 5.1 and the vertical changes as seen in Figs. 5.3 to 5.5 the distribution of the fauna in this area can be examined.

Distribution Of Individual Taxa (Untransported)

The distribution data are derived from disturbed neighbourhood assemblages, rather than the transported assemblages of the shell beds and the shells at the base of sandstone units, since the former assemblages are considered to most closely reflect the original distribution of faunas.

An attempt is now made to explain the distribution of the faunas (unmodified by transport) using data on the palaeoenvironment as derived from sedimentological studies and the autecology of each form as derived from studies of functional morphology.

In this section the distributions of fossil taxa are outlined in a brief prose description, this is not meant to accurately describe the distribution of each species, since this is given in the tables and diagrams presented below, but to emphasise the main aspects.

It should be noted that no fossils were found in the Trichrug Beds and the only fauna found in the lower Bringewoodian Carn Powell Facies of the Sawdde section and the lower Bringewoodian Grammysia Beds of the Cennen section had obviously been transported. Transported assemblages are considered separately in a later section.

P. ludloviensis. Although absent throughout the strata examined in the Gwydderig area P. ludloviensis is common in the upper Eltonian of the Sawdde and Cennen areas. These latter strata are considered to represent very nearshore environments in which turbulence was high and salinity low and variable. As noted on p. 19 P. ludloviensis appears to be well adapted to such nearshore environments which may not have been fully marine. In the Cennen sample F5 P. ludloviensis is suddenly extremely abundant both in terms of abundance relative to other species and in terms of density (Fig. 5.5). Such a pattern of occurrence is typical of an opportunistic species, which characteristically typify high stress environments (Levinton 1970) such as the one inferred for the deposits from which this sample originates.

M. nucula. This species is present in the upper Eltonian and lower Bringewoodian of the Gwydderig section and is common in the upper Eltonian of the Sawdde and Cennen valleys and the upper Bringewoodian of the Gwydderig section. Its increasing abundance towards shallower, more turbulent and fluvially influenced environments is consistent with its

adaptation to such conditions (p. 16).

S. lunata. Although absent from the strata examined in the Gwydderig section S. lunata is the dominant species in the upper Eltonian of the Sawdde and Cennen valleys. Its abundance in these nearshore turbulent and more fluvially influenced environments is consistent with its apparent adaptation to nearshore waters which may not be fully marine (p. 18).

I. orbicularis, I. clivosa. The latter species is very rare and occurs only in the upper Eltonian and upper Bringewoodian of the Gwydderig section. The former is the dominant species of the lower and upper Bringewoodian strata of the Gwydderig section and is the second most abundant species in the upper Eltonian of this section. Its absence from the more turbulent and fluvially influenced nearshore environments seen in the Cennen and Sawdde sections examined in this study is very marked. Its ecological niche in these environments is possibly taken by the very similar species S. lunata which is very well adapted to such conditions (p. 18). Although I. orbicularis is not adapted to such nearshore conditions, it is well adapted to the fairly turbulent although more offshore and less fluvially influenced environments (see p. 18), such as those represented in the Gwydderig section, where it is abundant. I. orbicularis was therefore confined to more offshore waters because it was intolerant of very turbulent and, or more probably (p. 18), not fully marine water. I. orbicularis was far more successful than I. clivosa.

S. wilsoni. This species shows an increasing abundance in progressively more nearshore environments. It is relatively rare in the upper Eltonian of the Gwydderig section, quite common in the lower Bringewoodian and upper Bringewoodian of the Gwydderig section and the upper Eltonian of the Cennen Valley and abundant (the second most common species) in the upper Eltonian of the Sawdde section. Such a distribution suggests a preference for nearshore conditions probably of quite high turbulence and low and variable salinity. S. wilsoni is certainly very well adapted for conditions of high turbulence (p. 15, 16). However, its absence from the uppermost Ludlow in the Welsh Borderlands which was deposited in a turbulent nearshore environment in which salinities may have been low or variable suggests it may not have been tolerant of anything but fully marine conditions. However, on Gotland S. wilsoni does extend into the uppermost Ludlovian which is again considered to have been deposited in a nearshore environment of high turbulence and low and variable salinity (Stel & Coo 1977) which suggests

it was quite euryhaline. Ager (1965) considered that Mesozoic rhynchonellids were tolerant of reduced salinities. Its absence from the uppermost Ludlovian in the Welsh Borderland remains enigmatic but appears not to be related to low salinity. In conclusion S. wilsoni appears to be well adapted to the turbulent waters and low and variable salinities of the nearshore environment.

A. reticularis. This species is abundant in the offshore, although moderately turbulent, environments of the upper Eltonian and lower Bringewoodian of the Gwydderig section, rare in the more nearshore upper Bringewoodian of the Gwydderig section and absent from even nearer shore environments. Its absence in the more nearshore waters is possibly due to a lack of adaptation to very turbulent conditions and or fully marine waters. Its abundance in the moderately turbulent, probably fully marine environments was due to its excellent adaptation (p. 12) to such conditions.

L. filosa. This species is common or quite common in the more offshore environments represented by the upper Eltonian to upper Bringewoodian of the Gwydderig section and the upper Eltonian of the Cennen but is rarer in the more nearshore conditions represented by the upper Eltonian of the Sawdde. Although well adapted to moderately turbulent conditions (p. 14) such as those of the former setting, L. filosa was not well adapted to very turbulent conditions (p. 14) and low and variable salinities which existed in the latter environment.

H. elegans. This species has rather a sporadic distribution. It is found rarely in the upper Eltonian and lower Bringewoodian of the Gwydderig section but was commoner, although not abundant in the nearshore environment of the Sawdde upper Eltonian. It is therefore commoner in the more turbulent, possibly low and variably saline waters of the latter environment to which the shell appears to be well adapted (p. 20).

L. depressa, S. euglypha, M. cf. lepisma. These 3 species have a similar distribution, they are all confined to the upper Eltonian and lower Bringewoodian of the Gwydderig section. The latter 2 species are very rare and the former uncommon in these strata. As discussed on p. 14, 15 L. depressa and S. euglypha are well adapted to quite turbulent conditions, suggesting their absence from the more inshore environments in this region may be due to variable salinity resulting from a strongly fluvial influence. However M. cf. lepisma is not well adapted to turbulent conditions (p. 13) so that its absence from the nearshore environments may be explained by strong turbulence and or low and variable salinity.

Bivalves. Bivalves are entirely absent from the upper Eltonian to upper Bringewoodian strata examined in the Gwydderig section and they are uncommon (one endobyssate suspension feeding form - Pteronitella sp. - and various indeterminate taxa make up less than 1.5% of the total fauna) in the more inshore waters of the upper Eltonian of the Cennen section. Bivalves only become abundant (forming over 20% of the total fauna) in the upper Eltonian of the Sawdde section. The bivalve fauna of this latter section is dominated by Pteronitella sp., which forms over 18% of the total fauna, the rarer bivalves consist of one other endobyssate suspension feeder (Modiolopsis sp.), one deposit feeder (Nuculites) and indeterminate forms.

Since filter feeding bivalves are absent from turbid environments due to resuspended mud particles clogging their filtering apparatus (Rhoads & Young 1972; Steele-Petrović 1975) the abundance of filter feeders in these strata suggest that the waters of this area were not turbid.

Hallam (1965), Sutton et al. (1970), Stanley (1972), Bowen et al. (1974), Thayer (1974), Rhoads (1975), Watkins (1978a) and Steele-Petrović (1979) have all noted that Palaeozoic bivalves have their highest abundance where the environment exerted stresses that imposed restrictions on other invertebrates; e.g. the nearshore environment. The nearshore setting in the Sawdde upper Eltonian was probably an environment of variable and at times high sedimentation rates (due to the unpredictable nature of overbank and crevasse deposition), extensive reworking by waves, strong wave buffeting and turbulence and low and variable salinity. The endobyssate bivalves were semi-infaunal forms capable of burrowing or reburrowing if exhumed by, for example, wave action, and were therefore well adapted to such an environment. The eurytopic nature of bivalves probably accounts for their abundance in this environment (e.g. Stanley 1972).

Trilobites. D. myops is present but rare in the upper Eltonian and lower Bringewoodian of the Gwydderig section. It was probably a nekto-benthic scavenger, predator or deposit feeder (p. 35, 36). Its absence from the more nearshore environments may be because the turbulence was too high, the salinity too low or variable or its prey too rare.

Proteus sp. occurs rarely in the upper Eltonian of the Cennen section. The mode of life of proetid trilobites is problematical (p. 36) and from morphological studies there are no apparent explanations for their distribution (Owens, pers. comm. 1978).

In the upper Eltonian of the Cennen section a homolonotid trilobite is quite common; these were burrowing forms which appear to have been adapted to such nearshore sediments (p. 36) thus accounting for their presence here.

Ostracods. Ostracods were only found rarely in the upper Eltonian of the Gwydderig section; conditions were obviously unfavourable for them. They are considered to have been benthic living on algal foliage (p. 37). Ostracods often show a complex relationship with algae (p. 37) and it is possible that the algae to which these ostracods were adapted was absent from this area. However conditions may have been unsuitable for the ostracods themselves.

Bryozoans. Bryozoans are quite common in the upper Eltonian and lower Bringewoodian of the Gwydderig area but are absent from sediments representing more inshore environments. Modern bryozoans are almost all fully marine forms, which require firm substrates, good water circulation and not too much turbulence (p. 30). In the nearshore zone there are no signs that water circulation was poor or the waters turbid (since filter feeding bivalves are abundant) and the shells of other organisms indicate the presence of firm substrates, therefore it seems likely that the high turbulence and low and variable salinity were responsible for the absence of bryozoans in these areas.

Gastropods. L. obsoletum forms a very small proportion of the fauna in the upper Eltonian of the Sawdde section. This slow moving epifaunal herbivore (p. 34) was probably responsible for some of the grazing trails seen in the siltstones of this section. This species appears to have been well adapted to such nearshore settings which may not have been fully marine (p. 34).

Tentaculitids. T. ornatus and Tentaculites sp. occur very rarely in the upper Eltonian and upper Bringewoodian respectively, of the Gwydderig section. Conditions were clearly unsuitable for them.

Crinoids. These occur rarely but consistently as scattered ossicles in most collections. The presence of echinoderms in the nearshore environments where the salinity is thought to have been low and variable is odd since echinoderms are usually confined to fully marine waters (e.g. Hallam 1965). However, crinoid ossicles are very light in weight and may have been transported from more marine environments further offshore (transported assemblages are discussed below).

Conclusion. By examining the functional morphology of individual taxa (Chapter 2) it is possible to explain the distribution of each taxon in the Llandovery-Llandeilo area in terms of its adaptation to different environments as deduced from sedimentological studies.

Transported Assemblages

The fauna of the transported assemblages were not discussed in the previous section since an attempt was being made to determine the original, primary, distribution of the fauna (unmodified by transport). In the Llandovery-Llandeilo area transported assemblages are confined to units interpreted as storm deposits and crevasse splay or levee sands.

The relative abundances of taxa in these transported assemblages relative to those of the disturbed neighbourhood assemblages in the surrounding sediment and the presence of species in transported assemblages which are otherwise unknown in the strata of the area concerned, will both help indicate the amount of transportation to which transported assemblages have been subjected.

In the upper Eltonian and lower Bringewoodian strata of the Gwydderig section the transported faunas of the storm deposits do not contain any species which are unknown from the disturbed neighbourhood assemblages of the surrounding sediments, indicating that shell transport has not been extensive enough laterally to mix different faunal assemblages. However, the rarer faunal elements of the disturbed neighbourhood assemblages are absent in the transported assemblages and the proportions of the taxa in the former type of deposit are different from those in the latter, presumably because of shell sorting and differential fragmentation due to transportation. This means, for example, that although I. orbicularis and A. reticularis are almost equally abundant in the disturbed neighbourhood assemblages from the Gwydderig upper Eltonian (their mean relative abundances being 36.39% and 36.50% respectively, Table 5.1), the transported assemblages from the same strata contain A. reticularis far in excess of I. orbicularis (their mean relative abundances being 49.93% and 24.43% respectively, Table 5.1). Another example is the abundance of these same 2 species in the lower Bringewoodian of the Gwydderig section; the mean relative abundances of A. reticularis and I. orbicularis being 24.44% and 47.56% respectively in the disturbed neighbourhood assemblages, but 47.93% and 36.03% respectively in the transported assemblages. Therefore a sample from a transported assemblage would give the false impression that A. reticularis was far commoner than I. orbicularis in these rocks. These facts suggest that although some shell transport and sorting has taken place im these storm deposits it has not been extensive enough laterally to introduce foreign species into the area.

The effects of more extensive shell transport are seen in the transported assemblages of the upper Eltonian strata of the Sawdde and

Cennen areas. Again the abundance of the taxa in the transported and disturbed neighbourhood assemblages are very different (Table 5.1), presumably due to shell sorting and differential fragmentation during transportation. For example in the upper Eltonian of the Cennen area the mean relative abundances of M. nucula and P. ludloviensis are 14.28% and 15.41% respectively in the disturbed neighbourhood assemblages, but are 25.76% and 6.54% respectively in the transported assemblages. A further example from the upper Eltonian of the Sawdde section is that the mean relative abundance of S. lunata, S. wilsoni and Pteronitella sp. are 26.38%, 20.89% and 18.16% respectively in the disturbed neighbourhood assemblages, but are 41.50%, 13.73% and 1.36% respectively in the transported assemblages. Moreover, in both these sections the transported assemblages contain many species which are unknown in the disturbed neighbourhood assemblages of the surrounding strata. In the Sawdde section there are 12 species and in the Cennen section 19 species (respectively 50% and 61% of the total number of species found in these strata) which are known only from transported assemblages. Some of these 'foreign' species are quite abundant, for example the mean relative abundances of I. orbicularis, C. implicata and solitary coral sp. B are 10.94%, 1.89% and 1.62% in the transported assemblages of the Cennen upper Eltonian. A sample from such transported assemblages would mistakenly imply that some species were present, or even lived quite commonly in this area when in fact the remains of such species in this area result only from shell transport.

Therefore we can conclude that the recognition of transported assemblages is vital since a sample taken from them may give totally wrong impression of the abundance or even presence of a species.

Finally it should be noted that the only fossils found in the lower Bringewoodian of the Sawdde and Cennen valleys are from transported assemblages. Since there are no known disturbed neighbourhood assemblages from these strata to compare them with, the amount of transportation and sorting which has occurred is unknown. However, the above discussion indicates that the composition and the relative abundance of the various members of the fauna of these assemblages may have been significantly altered by transport and no great reliability should be placed on them as representing the fauna which actually lived in these areas at this time.

Faunal Assemblages In The Llandovery-Llandeilo Area

Assuming that the correlation in Fig. 5.1 is correct, Calef & Hancock (1974) in their work on Ludlow 'communities' collected no samples from the Bringewoodian of the Llandovery-Llandeilo region and only two

samples, which they assigned to the 'Salopina community', from the upper Eltonian (in the Sawdde section). Since Calef & Hancock (1974, p.779) state that they never took more than 0.2 m of strata for any one collection it follows that they examined a total thickness of only 40 cm of rock from the upper Eltonian and Bringewoodian in the Llandovery-Llandeilo area, which is only 0.2% of the 167 m of strata examined from this area during the present study.

Calef & Hancock's 'Salopina community' differs quite substantially from the disturbed neighbourhood assemblages recorded here from the same level in the Sawdde section. An abundance of bivalves was observed in collections made by the author from these deposits, with non-brachiopods making up 25% of the total fauna (Table 5.1). However because Calef & Hancock only examined brachiopods, this important point went unnoticed. As Lawson (1975) noted the consequence of ignoring the non-brachiopod component of the fauna is that the proportion of faunal elements in Calef & Hancock's (1974) 'communities' are significantly altered. This is especially true in this case since the non-brachiopod content of the fauna is so high.

Moreover, 14 of the 20 brachiopod species Calef & Hancock (1974, p.784) record from the 'Salopina community' were not recorded from the disturbed neighbourhood assemblages of the Sawdde, despite the fact that a more intensive search of the beds was made than was undertaken by Calef & Hancock (1974). Since a further 4 of the 'Salopina community' species were found during this study to be confined to transported assemblages it seems possible that Calef & Hancock may have established the composition of their 'communities' partly on transported collections (they certainly do not mention recognising such assemblages in their work); a very questionable procedure in view of the discussion on transported assemblages above. However, other species listed in the 'Salopina community' (Calef & Hancock 1974, p.784), were not found in the untransported disturbed neighbourhood assemblages of the Sawdde (originating from the same level Calef & Hancock record the 'Salopina community' from) during this study, and appear to owe their presence in this list to their 'lumping' of collections from different sediments, with different faunas, into a single 'community'. For example Calef & Hancock lumped samples from the Leintwardinian of Usk with what are here regarded as upper Eltonian Sawdde samples, despite the fact that the former represents an offshore environment and the latter a nearshore fluvially influenced one; i.e. two completely different environments with different limiting factors and therefore different faunas were

not differentiated. The assignment of this Leintwardinian sample to the 'Salopina community' by Calef & Hancock probably goes a long way towards explaining the surprising abundance in this 'community' of D. navicula which is adapted to quiet distal shelf environments and not very proximal, turbulent, fluvially influenced ones (p. 20). By lumping together the collections from different sediments with different faunas Calef & Hancock (1974) obscure a more precise picture of the fauna which could otherwise be established, by more careful analysis.

Further criticisms of Calef & Hancock's work were given by Lawson (1975) and discussed herein (p. 89, 90). Lawson (1975) did not describe the faunal associations of this area, since he recognised that the area constituted an unusually sandy variety of the shelf facies; however he did note that the fauna was different from the typical shelf facies.

Recently Squirrell & White (1978) have investigated the Cennen Valley sections and assigned their faunal collections to Calef & Hancock's communities, rather than Lawson's (1975) assemblages, since they claim that their collections fit better into the former scheme. This is probably because a large number of Calef & Hancock's collections came from the Llandovery-Llandeilo area, with its atypical facies and fauna (compared to the shelf) while none of Lawson's (1975) assemblages were based on data taken from this region. Squirrell & White record the upper Coed Wenallt Beds as having a 'Sphaerirhynchia community' while the Grammysia Beds yielded a 'Salopina community'.

Therefore until this study only a few widely scattered samples had been collected from some sections in the upper Eltonian and Bringewoodian strata of this region and these had been lumped into 'communities' which included collections from different sediments representing different environments with different faunas.

It is clear therefore that a confused picture of the faunal distribution in this area has emerged because no attempt has been made to distinguish between transported and untransported assemblages and relate the latter to the palaeoenvironment which can be inferred from sedimentological work.

The lumping of fossil collections into communities has obscured a more complex faunal distribution which has here been shown to exist by detailed bed-by-bed sampling and careful analysis of the data. By examining the sediments and functional morphology of individual taxa it has proved possible to explain their distribution in terms of their adaptation to different environments as deduced from sedimentological studies.

The procedure outlined above is considered essential for interpreting the distribution of species in a stratigraphical unit, however, further valuable information may be gained by recognising the existence of loose faunal assemblages. Information on such assemblages found in the strata of the Llandovery-Llandeilo area during this study are given below. The descriptions are necessarily very general ones since there is quite noticeable variation within each one. Data for these descriptions is derived from disturbed neighbourhood assemblages (which are thought to be closest in composition to the original faunas) and not the transported assemblages which show signs of selective transport and introduced 'foreign' species into the area. However, in the case of the lower Bringewoodian of the Sawdde and Cennen valleys only transported faunas are known, these are noted below but it is stressed here that the obtainable information on species occurrence and abundance is almost certainly, to some extent, misleading.

Density is given as the average number of individuals per 5000 cm^3. Diversity is given both as the average number of species which would be found in a collection of 100 individuals from that assemblage and also the average number of species found in collections from that assemblage (the latter index is indicated by an asterisk above the figure).

upper Eltonian-Gwydderig-upper Black Cock Beds (in part). The fauna is dominated by large thick shelled brachiopods (A. reticularis) and pedically attached forms (I. orbicularis), large but thin shelled forms (L. filosa) are less common. Faunal density is moderate (50) but diversity is low (9, 10 *).

upper Eltonian-Sawdde-upper Black Cock Beds. The fauna is dominated by large, thick shelled, pedically attached brachiopods (H. elegans, M. nucula, S. wilsoni), other pedically attached brachiopods (S. lunata), the unattached form P. ludloviensis and many bivalves, especially Pteronitella sp. Faunal density (5) and diversity (6*) are very low.

upper Eltonian-Cennen-upper Coed Wenallt Beds. The fauna is similar to that found above except that bivalves are uncommon and L. filosa is moderately common. Faunal density (6) and diversity (9, 7 *) are very low.

lower Bringewoodian-Gwydderig-upper Black Cock Beds (in part). The fauna is dominated by a group of large thick shelled and or pedically attached forms (A. reticularis, I. orbicularis, S. wilsoni). Faunal density is moderate (36) and diversity low (10, 10 *).

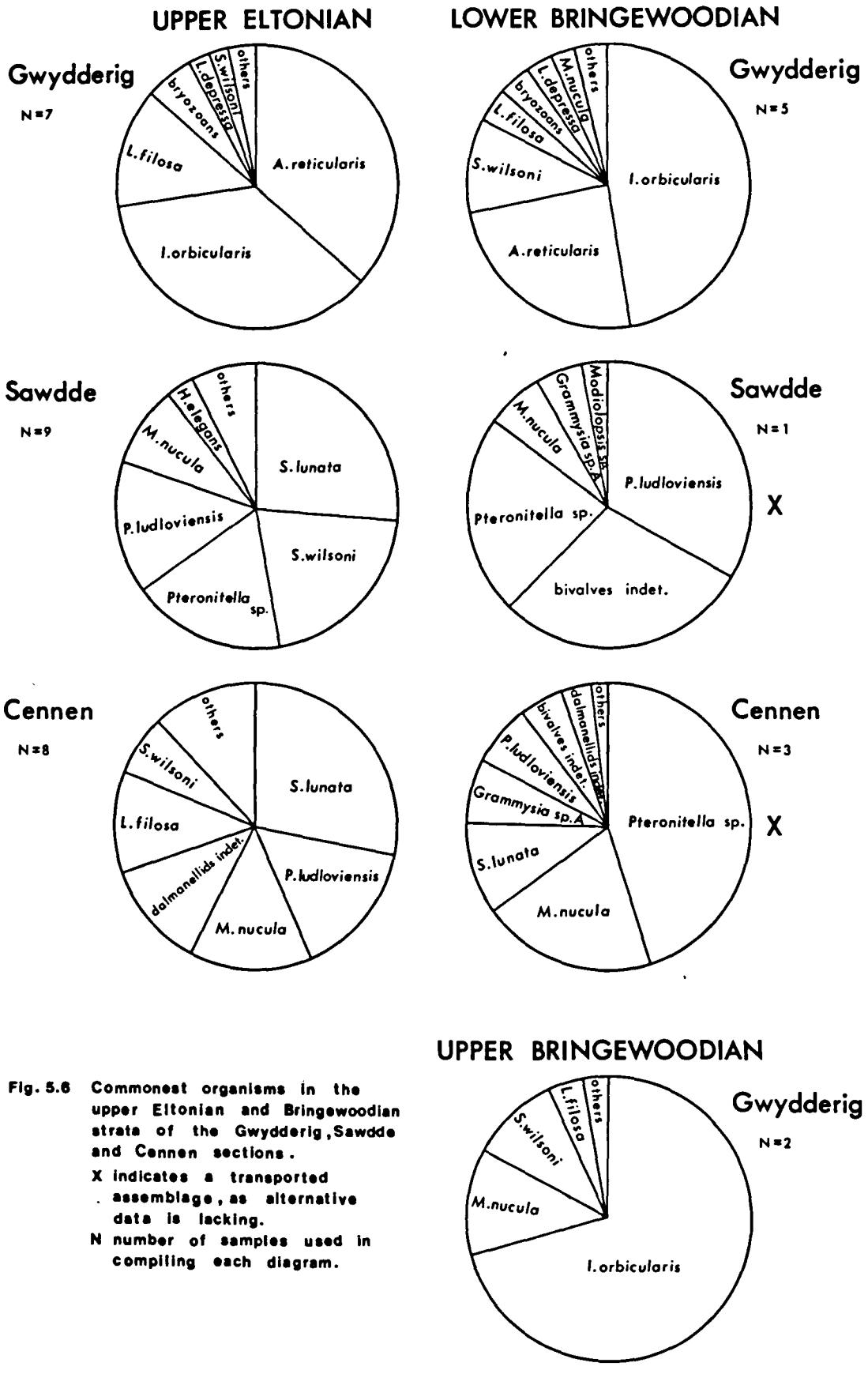

Fig. 5.6 Commonest organisms in the upper Eltonian and Bringewoodian strata of the Gwydderig, Sawdde and Cennen sections.

X indicates a transported assemblage, as alternative data is lacking.

N number of samples used in compiling each diagram.

lower Bringewoodian-Sawdde-Carn Powell Facies. There are no body fossils which do not show signs of transportation in these strata. A single transported assemblage has been recovered from these strata. In this bivalves and P. ludloviensis dominated. Density is moderate (50) but diversity is low (6, 6*).

lower Bringewoodian-Cennen-Grammysia Beds. Again the only faunas known from these strata are transported. Bivalves and M. nucula dominate. Density is extremely high (4680) due to concentration during transport, but diversity is low (9, 9*).

upper Bringewoodian-Gwydderig-lower Lower Cwm Clŷd Beds. The fauna is dominated by a group of pedically attached and or thick shelled forms (I. orbicularis, S. wilsoni, M. nucula). Density is fairly low (18) and diversity low (7, 7*).

upper Bringewoodian-Sawdde and Cennen-Trichrûg Beds. Both transported and untransported faunas are apparently entirely absent.

The 7 assemblages discussed above are illustrated in Fig. 5.6.

Factors Controlling Faunal Distribution In The Llandovery-Llandeilo Area

Previous suggestions of factors controlling faunal distribution in the shelf Ludlow have already been discussed (p. 88-92) but a summary is given below. Calef & Hancock (1974) defined 5 brachiopod 'communities' from the Ludlow. They considered that there was no correlation between sediment type and 'community' and considered that an alleged decrease of food with depth was the controlling factor on brachiopod distribution. Although, Hancock et al. (1974) considered that these 5 'communities' had a depth range of 1500 m, Shabica & Boucot (1976) argued that it was probably more like 200 m. If the latter figure is correct then it is extremely unlikely that a variation of food with depth controlled the distribution of fauna in the Ludlow, as Calef & Hancock (1974, p.803) suggested, since Hallam (1965) and Rhoads (1975) have argued that it is improbable that food was a limiting factor for suspension feeders in epeiric seas.

Lawson (1975) strongly criticised the work of Calef & Hancock (1974). He noted that some of Calef & Hancock's collections had been assigned to the wrong divisions of the Ludlow, that potential controlling factors on faunal distribution were not necessarily depth controlled, that by ignoring the non-brachiopod benthos Calef & Hancock had significantly altered the proportion of faunal elements in their 'communities' and that their sample coverage was poor and widely spaced. Furthermore, Cherns

(1979) noted that 3 of Calef & Hancock's (1974) 'communities' alternated in less than 1 m of Lower Leintwardinian strata. She argued that since it was impossible to envisage sudden pronounced depth changes (of many tens of metres at a minimum cf. Shabica & Boucot (1976) or hundreds of metres at a maximum cf. Hancock et al. (1974)), occurring over such a short distance; Calef & Hancock's communities cannot be depth related in the manner they suggest. Watkins (1975, 1979) has argued that only when depositional environments parallel bathymetry do 'communities' occur in depth related bands, if environmental zones do not parallel bathymetry then benthic 'communities' show a similar lack of depth relation.

Fursich & Hurst (1974) attempted to relate lophophore size to the depth of water inhabited by various Silurian brachiopods, assuming that less food existed in deeper water, although Hallam (1965) and Rhoads (1975) have argued that food was not a limiting factor in epeiric seas. Moreover, it appears that brachiopods can adapt their shells to live in almost any suitable environment irrespective of their lophophore size; the hypothesis therefore appears untenable (see p. 91, 92 for further discussion).

As Lawson (1975) noted, the emphasis on 'depth communities' has led to the neglect of other factors, e.g. substrate type, which affect faunal distributions.

It was concluded therefore (p. 92, 93) that in this study the morphological features of each taxon and the environmental factors deduced from sedimentological evidence should be considered before the most important features of each were assessed. From such an approach it was possible to account for the observed distribution of each species in the Llandovery-Llandeilo area (and indeed in the shelf and basin facies). This approach is also adopted now in an attempt to explain the distribution of faunal assemblages (described in the previous section) in the strata examined during this study.

In the upper Eltonian the Gwydderig region probably lay on the outermost part of the delta platform or in the inner prodelta area. Sedimentation was relatively moderate and bioturbation quite extensive. Turbulence was quite high and the bottom sediments were reworked by currents. The fauna was well adapted to such conditions with a dominance of large, thick shelled and or pedically attached forms.

To the south-west an interdistributary bay environment has been inferred for the Sawdde region. Frequent reworking of the sediment, probably mainly by waves, is apparent and mechanical buffeting by waves may have been extensive. The proximity to alluvial distributaries suggests

that sedimentation rates were variable due to sudden overbank or crevasse deposition in times of flood and that salinity values were low and variable. The dominance of thick shelled, mainly pedically attached brachiopods, most of which were inferred in Chapter 2 to be tolerant of reduced or variable salinities, show good adaptation to such conditions. Semi-infaunal bivalves are also well adapted to such conditions, since they can burrow to avoid major environmental disturbances and were probably quite eurytopic (p. 163); they too are therefore well adapted to and dominant in such an environment. The absence of other groups (e.g. bryozoans, corals etc.) from this environment is probably primarily due to the low and variable salinity, the periodic heavy sedimentation and the high turbulence to which they were unsuited.

The Cennen area was situated in a nearshore deltaic platform region. Conditions here were probably similar to the Sawdde. No crevasse or overbank deposits are known however and conditions were probably less extreme; i.e. not those of an interdistributary bay but rather of an inshore deltaic platform area. However, sediment reworking and turbulence appear to have been high and salinities were probably low and variable due to the proximity of distributary channels. Again the fauna is well adapted to such a nearshore environment, with a dominance of robust, pedically attached and salinity tolerant brachiopods.

The change from upper Eltonian to lower Bringewoodian sedimentation was marked by progradation of the delta northwards. The effects of this progradation are well seen in the Cennen and Sawdde areas. However, the Gwydderig area appears to have been largely unaffected, with an environment identical to that of the upper Eltonian in this area, as inferred from the sediments. The fauna is also similar to that from the upper Eltonian of this same section, although a small increase in the more robust and pedically attached forms, perhaps implies an increase in turbulence which is not so apparent from the sedimentary investigations.

The Sawdde area now lay in a subaerially exposed, largely fluvially dominated distributary channel environment, although evidence (p. 154) shows that the area lay within the reach of tidal influences. The conditions appear to have been beyond the adaptive range of almost all organisms since only rare burrows are known and no indigenous shelly fossils were found. The only shells present are those at the base of a channel sandstone and have almost certainly been swept in from a more off-shore environment by either tidal or storm generated currents. The dominance of bivalves in the assemblage suggests a fairly nearshore environment, but this may be the effect of current sorting and concentration.

The Cennen area was now situated in an interdistributary bay which appears to have been similar, if not identical to the one that existed in the Sawdde area during the upper Eltonian, and environmental conditions are thought to have been similar. However, the absence of fauna, except for the transported assemblages, may imply that conditions were more extreme than the Sawdde setting, being therefore beyond the limit of adaptation of all organisms except those responsible for creating the few observed burrows. The fauna of the transported assemblages is very similar to that seen in the disturbed neighbourhood assemblages of the Sawdde interdistributary bay complex, which may suggest little transport for these deposits in this case. However, because transported assemblages may introduce foreign species into an environment and or markedly change the proportion of species actually present by current sorting and concentration it is unwise to place too much reliance on these assemblages, especially since no untransported fauna at all (except for a few burrows) is known from these strata.

Further northwards progradation of the delta resulted in the delta platform reaching well into the Gwydderig area by the upper Bringewoodian. The environment was quite turbulent with much reworking of the bottom sediments. The increase in turbulent conditions during the upper Eltonian and lower Bringewoodian in this area is reflected by an increase in pedunculate and more robust brachiopods which were well adapted to this more turbulent environment.

In the Sawdde and Cennen areas the existence of alluvial plain sedimentation excluded all organisms; apparently at this time there were no forms capable of adapting to such conditions.

The changes in faunal diversity seen in the assemblages of the Llandovery-Llandeilo area are explained by the existence of greater physiological stress reducing diversity in some environments (cf. Sanders 1968, 1969; Slobodkin & Sanders 1969; Sanders & Hessler 1969). Over the whole Llandovery-Llandeilo area, diversity is low compared to most of the Lower Bringewoodian of the shelf facies; this reflects the high stress conditions. The number of species per sample (of disturbed neighbourhood assemblages) is used in the following comparisons, since disturbed neighbourhood assemblages will be nearer the original fauna than transported assemblages and more data is available for number of species per sample, than rarefied data.

The sediments of the outermost delta platform have the highest faunal diversity (10) while inshore this drops to values of 6 or 7. The inshore environment was probably one of low and variable salinity, wide and

variable temperatures, high and or variable sedimentation rates, frequent reworking by tidal waves and currents and substantial wave buffeting. Low diversity is to be expected in such a stressful environment. Similar nearshore deltaic environments examined both from modern settings and inferred from ancient deposits also have low diversities, which have been attributed to the high stress conditions existing in them (Parker 1956; Sutton et al. 1970; Stanton & Evans 1972; Bowen et al. 1974; Rhoads 1975).

The high stress environment inferred to have existed nearshore is also thought to be responsible for reducing faunal density values; cf. 50 (per 5000 cm^3 of sediment) in offshore sediments with only 5 or 6 in the nearshore environments. Again low faunal densities in nearshore deltaic environments have been attributed to the high physical stresses exerted by such environments, both in modern deltas and ones interpreted from ancient sediments (Parker 1956; Sutton et al. 1970; Bowen et al. 1974).

Sanders & Hessler (1969), Johnson (1970, 1971), Rhoads & Morse (1971), Dörjes (1972), Jackson (1972) and Cisne & Rabe (1978) have all shown that faunal gradients reflect environmental gradients. Johnson (1972) has argued that if environmental gradients are gradual then communities will change gradually, but if sharp breaks exist in the environmental gradient then communities will appear discontinuous.

Therefore during the upper Eltonian the rather variable relative abundance of species (e.g. I. orbicularis in the Gwydderig, Pteronitella sp. in the Sawdde and M. nucula in the Cennen sections) suggests that the environmental conditions were variable at this time. Since these changes in the species relative abundance at this time is more pronounced in the Sawdde section than elsewhere; it appears that in this area the environmental conditions varied the most (a fact supported by sedimentological studies). These species are not really opportunistic (except perhaps P. ludloviensis, discussed on p. 160) in that their density is never large (i.e. indicative of a population explosion, cf. Levinton (1970)). Their relative abundance probably varies simply as a result of small scale variations in the environment or random variations in population development.

In the upper Eltonian, the overall upwards decrease of some species (e.g. S. wilsoni and S. lunata in the Sawdde section and A. reticularis and L. filosa in the Cennen section) while some species show an upward increase in abundance (e.g. Pteronitella sp. in the Sawdde section and M. nucula and S. lunata in the Cennen section) suggests that not only were minor fluctuations taking place in the environment but that the overall environment in these areas was also gradually changing during this time.

At the base of the lower Bringewoodian the sudden disappearance of any untransported fauna in the Sawdde and Cennen sections suggests a rapid change in the environment here to conditions beyond the adaptive range of apparently any organisms, except the presumably soft bodied fauna responsible for the rare bioturbation seen. However in the Gwydderig section the fauna changes only gradually from the upper Eltonian to the lower Bringewoodian (e.g. A. reticularis becomes less common) indicating only a gradual change in the environment. There is no indigenous fauna in the Bringewoodian of the Cennen and Sawdde valleys to use for this model but the base of the upper Bringewoodian in the Gwydderig section is marked (according to Price (1957)) by a gradual change in fauna, suggesting a gradual change in environment. However the junction was not observed by the present author.

The rapid or gradual changes in environment at this time correlate well with the sedimentological evidence and appear to be due to northward progradation of the delta in a series of 'steps'. The strong correlation of fauna and facies suggests an important control by the physical environment on faunal assemblages.

Conclusions

The distribution of the fauna in the Llandovery-Llandeilo region was controlled by a complex of physical environmental parameters such as variations in turbulence and wave buffeting, shifting of substrates due to reworking, sedimentation rates, salinity, temperature and exposure.

The proposal by Calef & Hancock (1974) and Fürsich & Hurst (1974) that variation in food supply with depth controlled faunal distribution in this area is rejected, since food supply is unlikely to have been a limiting factor in epeiric seas (Hallam 1965; Rhoads 1975); for the other reasons given above, the food and depth control hypotheses are further disputed.

Physical environmental changes influenced the qualitative and quantitative characteristics of faunal assemblages. As conditions became limiting for individual species they were excluded or became rare, while other species better adapted for the environment entered the fauna or noticeably increased in abundance. Species appear to occur together only where their environmental tolerances overlap. Therefore a large degree of species independence seems to have existed, although predators must have been limited by the distribution of their prey and ostracods may have been limited by the type of algae present.

In conclusion it appears that a whole complex of physical environmental factors controlled the faunal distribution at this level.

CHAPTER 6

SUMMARY AND CONCLUSIONS

COLLECTING TECHNIQUES

A bed-by-bed sampling technique was used in this study to ensure that a complete and representative picture of the geographical and stratigraphical distribution of both the fauna and lithology was obtained. A spaced sampling technique would have missed important data, since the fossils especially are often unevenly distributed throughout the strata, occurring both sporadically and concentrated as bands (e.g. storm deposits or the soles of turbidites).

Using a bed-by-bed sampling technique a comprehensive quantitative analysis of the lower Bringewoodian fauna was made. Percentage relative abundances for each taxon in each collection were calculated (so that all collections could be directly compared) as well as diversity and density measurements.

FAUNAL DISTRIBUTION

Charts were drawn up to accurately show the variation of the relative abundance of each taxon, the lithology, the faunal density and the faunal diversity between samples in each section (e.g. Fig. 3.7). By separating transported faunas (storm deposits and slump and turbidite faunas), which show varying degrees of sorting, from those faunas showing little or no signs of transport it was possible to establish the original faunal distribution more accurately.

Faunal variation within one section could be quickly and easily assessed by visual examination of the charts discussed above. Comparison of faunas in the different lithologies of one section and the same and different lithologies between sections was aided by calculating mean relative abundances for untransported and transported faunas in each lithology in each section (see p.73 for method of calculation). Gross relative abundance values were displayed in tables (e.g. Table 3.1).

STRATIGRAPHY

The ability to locate the Lower Bringewoodian or even the lower Bringewoodian throughout the study area proved to be one of the most difficult tasks of the project.

Identification of the Lower Bringewoodian in the shelf region, achieved mainly by analysis of the shelly benthic fauna, and to some extent by examination of lithologies is generally straightforward. Palynology and graptolite studies do not indicate any diachronism of the unit. However, in the basin and the Llandovery-Llandeilo area identification of the lower Bringewoodian is very difficult because the fauna and lithologies are so different from the type area.

It was hoped at the beginning of the project that graptolites, which are quite common in the basinal succession, would establish the basinal equivalents of the Lower Bringewood Beds. Unfortunately, it transpired that most of the graptolites were poorly preserved and unidentifiable. Even when they could be identified the finest resolution towards locating the lower Bringewoodian they could provide was identifying the incipiens (tumescens) Zone. Since three divisions of the Ludlow (upper Eltonian and, lower and upper Bringewoodian) are spanned by this zone it is not possible, from the graptolite evidence, to be certain whether the beds being examined were lower Bringewoodian in age. Therefore the middle third of the incipiens Zone was examined. This was obviously a very crude approach which assumed constant deposition of sediment over a long time period and equal lengths of time for these three Ludlow divisions. Fortunately, however, the lithology and indigenous fauna remains constant during the incipiens Zone in many basinal sections. Therefore even if the direct contemporaries of the Lower Bringewood Beds were not examined, the palaeoecological and sedimentological information collected from the strata examined were almost certainly identical to that obtainable from the true equivalent horizons.

The recognition of the lower Bringewoodian in the Llandovery-Llandeilo region is even more difficult than in the basin, since, not only was the fauna here strongly influenced by the atypical sandy nature of the sediments but also graptolites are rare and the correlation of this area with the graptolitic basin succession is unclear. Using some recent, sparse (but important) graptolite evidence (Squirrell & White 1978) and palynological evidence (Dorning pers. comm. 1978) a correlation scheme is proposed for this area (Fig. 5.1) which, it is argued, is the best that can be done with the available data. It is hoped that future work on palynology and ostracods will improve the accuracy of correlating this area with the type succession.

FUNCTIONAL MORPHOLOGY

To explain the distribution of the lower Bringewoodian fauna it was necessary to have a knowledge of the autecology of each taxon, deduced from a review of the functional morphology of each species. Information on the functional morphology of all lower Bringewoodian species was therefore collated and a summary of the main views presented in combination with this author's conclusions.

SEDIMENTOLOGY

Since the ultimate objective of this study is to interpret the fauna in terms of its environmental distribution, sedimentological studies were carried out in order to deduce the environments of deposition represented by lower Bringewoodian successions.

THE SHELF

During the Upper Eltonian over the whole of the shelf area low energy conditions prevailed with fine material settling out of suspension. The rarity of bioturbation suggests a restricted benthic fauna and less than fully oxygenated conditions, probably due to insufficient mixing of the water. Although, in more proximal areas, in the south-east, away from the shelf edge, bioturbation does increase indicating more benthos due to greater mixing of the water because of more turbulence.

The mainly pelagic and nektic fauna of graptolites and orthocones and the small size of the benthic fauna (mainly S. ludloviensis) reflect the unfavourable bottom conditions. Since small animals are well adapted to low oxygen levels (Raff & Raff 1970) and require less food per individual and because poor oxygenation implies a lack of currents, which would supply nutrients, a population of them would stand a better chance of survival in these conditions. The increase in the proportion of the benthic fauna and the decrease in the abundance of small species to the south-east is thought to reflect the increased mixing of water and therefore more favourable bottom conditions pertaining in this area.

At the base of the Lower Bringewoodian a major increase in turbulence resulted in the whole shelf becoming better oxygenated with benthic animals more able to burrow into and completely rework the slowly-deposited sediment to produce the bioturbated siltstone facies. Within this facies an environmental gradient is deduced between the quieter, distal sediments around the shelf edge and the more proximal deposits of the south-east where higher-energy, more-turbulent conditions prevailed.

The improved water circulation at the base of the Lower Bringewoodian was responsible for the appearance of corals and bryozoans. Paralleling the environmental gradient noted above is a gradual change in the composition of the fauna across the shelf. The fauna of the shelf facies was divided into three assemblages, although this was an artificial arrangement since they integrate laterally and are part of a continuum across the shelf (Fig. 3.12). The outer shelf assemblage is dominated by small, smooth, thin shelled, unattached brachiopods (e.g. S. ludloviensis) which were well adapted to the quiet water conditions, and the possibly below normal nutrient and oxygenation levels of the bottom waters which may have existed in these poorly circulated waters. The poor water circulation and low nutrient supply associated with it were probably responsible for the rarity and stunting of A. reticularis in these areas. Growth line studies reveal that individuals of this species become mature at about half the size of individuals from the proximal shelf, where it is the commonest species. The middle shelf assemblage shows a decrease in forms such as S. ludloviensis (which would be more easily swept away in the slightly more turbulent conditions deduced for this part of the shelf) and an increase in larger, thicker shelled, although, still mostly smooth and unattached brachiopods (e.g. M. cf. lepisma) which were better adapted to the slightly more turbulent environment. The inner shelf assemblage is dominated by large, thick shelled, strongly ribbed brachiopods (e.g. A. reticularis, S. wilsoni), many of which were pedically attached and are ideally adapted for the moderately turbulent conditions of this environment.

Occasionally during the Lower Bringewoodian quite turbulent conditions prevailed; these can be deduced from the development of a more nodular and calcareous facies - the nodular bioturbated siltstone facies. These relatively short-lived increases in turbulence are similar to those recorded in the Upper Bringewoodian by Newall (1966). The fauna of the nodular bioturbated siltstone facies reflects the higher energy conditions with an abundance of strong, large, thick shelled, robust brachiopods (e.g. A. reticularis, G. lata, S. euglypha); the increase in bryozoans and corals reflects the good water circulation and lack of turbidity.

During deposition of the Lower Bringewoodian storms periodically swept across the shelf throwing sediment into suspension and scouring the fauna from the sea bed and depositing it as shell beds in storm deposits. A low degree of scouring is indicated by the virtual absence of infaunal species in these deposits. Some taxa, showing marked concentration or

depletion in these storm deposits, indicate some degree of sorting. Storm deposits are commonest in the more proximal areas and less common in the distal outer shelf region where their effect on the sediment and fauna was noticeably diminished.

At the base of the Upper Bringewoodian a further major increase of turbulence in the depositional environment led to the formation of the most calcareous phase of the Ludlow. Deposition over the whole shelf was now in quite shallow water, probably above wave base. In these clear, shallow, well circulated waters corals thrived, at times forming reef like masses, although large, thick shelled, robust brachiopods (e.g. A. reticularis, S. euglypha) well adapted to the high energy environment still dominate the fauna.

THE BASIN

Beyond the shelf edge to the north-west likes the basin, a north-north-east trending fault controlled trough. The basin area subsided faster than the surrounding area to accumulate about 4 to 8 times as much sediment as the average (40 m) shelf thickness in the lower Bringewoodian. Since the basin contains slumps and turbidites derived from the shelf edge and upper slope regions, its bottom must have been at a greater depth of water than that covering the shelf, although its exact depth is uncertain.

During most of the lower Bringewoodian (and upper Eltonian) parallel laminated flags accumulated in the basin. These sediments are identical to modern and ancient examples, either forming or considered to have formed in uncirculated, very poorly oxygenated bottom waters which excluded benthic life so that (annual) laminations were not disrupted by bioturbation or bottom currents. It is therefore considered that active tectonic subsidence of the fault controlled trough floor had taken it beyond the reach of normal surface circulation so that the bottom waters became poorly oxygenated. No evidence of trace fossils or bottom currents disturbing the regular (possibly annual) laminations of the parallel laminated flags was found. L. lata appears to have been the only indigenous benthic species and apparently it tolerated the conditions of poor oxygenation, nutrition, constant sedimentation and high turbidity which are inferred. It is not suggested that these bottom waters were anoxic but that the oxygen levels were below those tolerated by virtually all benthos (i.e. about 0.1 ml/l (Rhoads & Morse 1971)). Cherns (1979) has already suggested that L. lata was tolerant of turbidity, sedimentation and low oxygen levels. The remaining fauna of the parallel laminated flags was

either holoplanktic (graptolites), nektic (orthocones), epiplanktic (P. tenuistriata and C. cornucopiae) or epifaunal, perhaps attached to benthic shelf algae which were swept into the basin by possibly storm currents (S. wilsoni, M. nucula, A. grayi). The bedding planes covered by graptolites or P. tenuistriata are considered representative of gregarious sunken masses of these taxa, since the apparently continuous nature of basin sedimentation makes it extremely unlikely that they represent breaks in deposition. In the case of P. tenuistriata the planes probably represent the settling of the sunken algae to which they were attached. Size frequency analysis, ratio of opposing valves in different size categories and orientation analyses on 5 well preserved P. tenuistriata planes suggest, contrary to Straw's (1937, p.413) claim, no current activity in the environment of deposition.

On the basin slopes sediment slumped down and accumulated at the slope/floor break whilst turbidites flowed northwards along the basin floor. The thinness of the basin facies lower Bringewoodian (17 m) in the Knill area is considered to result from this upper slope area acting as the source for all north-north-west flowing turbidites and many of the eastern margin slumps at this time (Bailey 1969). Generation of slumps and turbidites was probably in response to movements along the faults controlling the basin slopes. These turbidites and slumps occasionally brought a displaced rich shelly benthic fauna from the shelf edge regions into the basin areas or a sparse fauna from the basin itself. In the uppermost regions of the basinal slopes (e.g. Knill) rare distal storm deposits are found; these contain a transported fauna from the shelf edge regions.

Towards the end of the lower Bringewoodian (and into the upper Bringewoodian) north-north-east flowing bottom currents, apparently originating from the Llandovery area reached the Builth Wells and Cwm Graig Ddû region and water circulation improved resulting in a more oxygenated bottom environment. However, conditions were still very quiet in these distal areas and the bottom waters were probably not fully oxygenated or supplied with nutrients so few benthic species could adapt to them. A restricted indigenous benthic fauna of D. navicula, L. lata and annelids (?) existed, the remaining fauna constituted holoplanktic graptolites, nektic orthocones, epiplanktic P. tenuistriata and C. cornucopiae and species which may have been epifaunally attached to shelf benthic algae which were swept into the basin by strong currents or storms (M. nucula, S. wilsoni). Both the benthic fauna and the bottom currents were responsible for disrupting the laminations of these beds - the irregular laminated flags.

Distal storm effects rarely reached these areas. The absence of slumps and turbidites in the irregular laminated flags indicates a more stable tectonic environment in these areas during the deposition of these sediments.

THE LLANDOVERY-LLANDEILO AREA

To the south-west the basin deposits grade into shallow marine and alluvial deposits.

During the upper Eltonian the Gwydderig area constituted an outer delta platform or inner prodelta environment in which various sediments, including storm deposits and probably river generated turbidites accumulated. Reworking of sediment occurred and turbulence was probably moderate; the fauna was well adapted to such conditions with a dominance of large, thick shelled or pedically attached brachiopods (e.g. A. reticularis, I. orbicularis). Due to sorting the proportion of faunal elements is different in the storm deposits. To the south-west an interdistributary bay environment existed in the Sawdde region. In this bay, overbank, levee, crevasse splay and storm deposits accumulated. Crevasse or tidal channels cut through these deposits. In this environment, waves frequently reworked the sediment and mechanical buffeting by waves was probably extensive: sedimentation rates and also probably temperatures were variable and salinity values low or variable. The relatively untransported fauna was well adapted to such conditions with a dominance of pedically attached brachiopods, probably tolerant of variable salinities (e.g. S. lunata, S. wilsoni), and semi-infaunal bivalves (e.g. Pteronitella sp.). The transported assemblages (crevasse splay and storm deposits) of these strata show not only different proportions of faunal elements due to sorting but also the introduction of many foreign species into the area. Further south-west in the Cennen area the environment was that of a nearshore delta platform. Reworking of sediments and turbulence were high and salinities low and variable due to the proximity of distributary channels. The relatively untransported fauna was well adapted to such an environment with an abundance of pedunculate brachiopods tolerant of variable salinities (e.g. S. lunata, M. nucula). The transported fauna of these strata show that shell transport has altered the proportion of faunal elements and introduced foreign species into the area.

During the lower Bringewoodian the environment in the Gwydderig area remained largely unchanged and the fauna remained similar. However, the effects of delta progradation are seen further south-west. In the Sawdde region an area of tidally influenced distributary channels then

existed. These channels appear to have often changed their courses; transported shells were rarely swept into them by storms or tides. To the sides of the channels overbank, levee and crevasse splay deposits accumulated. Exposure was probably high and temperature and salinity variable. Such conditions appear to have been beyond the adaptive range of all animals, except those responsible for the rare burrows (annelids?). In the Cennen area a shallow water interdistributary bay was being filled with overbank, levee and crevasse splay deposits. Sediment reworking, buffeting by waves, variable sedimentation, temperature and variable salinities probably all combined to produce an environment which appears to have been beyond the adaptive range of all animals, except those responsible for the rare burrows (i.e. annelids?). The only shelly fauna is a transported one found in crevasse splay deposits.

In the upper Bringewoodian the effects of further delta progradation can be seen in all sections. The Gwydderig region now lay well onto the delta platform, sediment reworking and turbulence were probably high and the fauna, with its abundance of pedunculate and robust brachiopods (e.g. I. orbicularis, S. wilsoni, M. nucula), reflects this. In the Sawdde area braided rivers deposited sediment on a delta plain, while in the Cennen region alluvial deposits accumulated near the area of provenance; the conditions in these areas were too harsh for any life forms.

SUMMARY

A reconstruction of the lower Bringewoodian palaeogeography in the area studied in this work is presented in Fig. 6.1.

CONTINUOUS REGRESSION

Continuous regression throughout the Ludlow, as proposed by Calef & Hancock (1974) and reiterated by Watkins (1975, 1979) and McKerrow (1979), is rejected for both the shelf and Llandovery-Llandeilo areas. There is abundant sedimentological evidence to suggest that the relatively shallow water Bringewoodian rocks in these areas are overlain by deposits of deeper water environments (Price 1957; Potter 1960; Holland & Lawson 1963; Potter & Price 1965; Phipps & Reeve 1967; Lawson 1975; R. Marsh 1976; Cherns 1977).

FAUNAL ASSEMBLAGES

Previous palaeoecological work by Calef & Hancock (1974), Lawson (1975) and Watkins (1975, 1979) has suggested that the shelf fauna

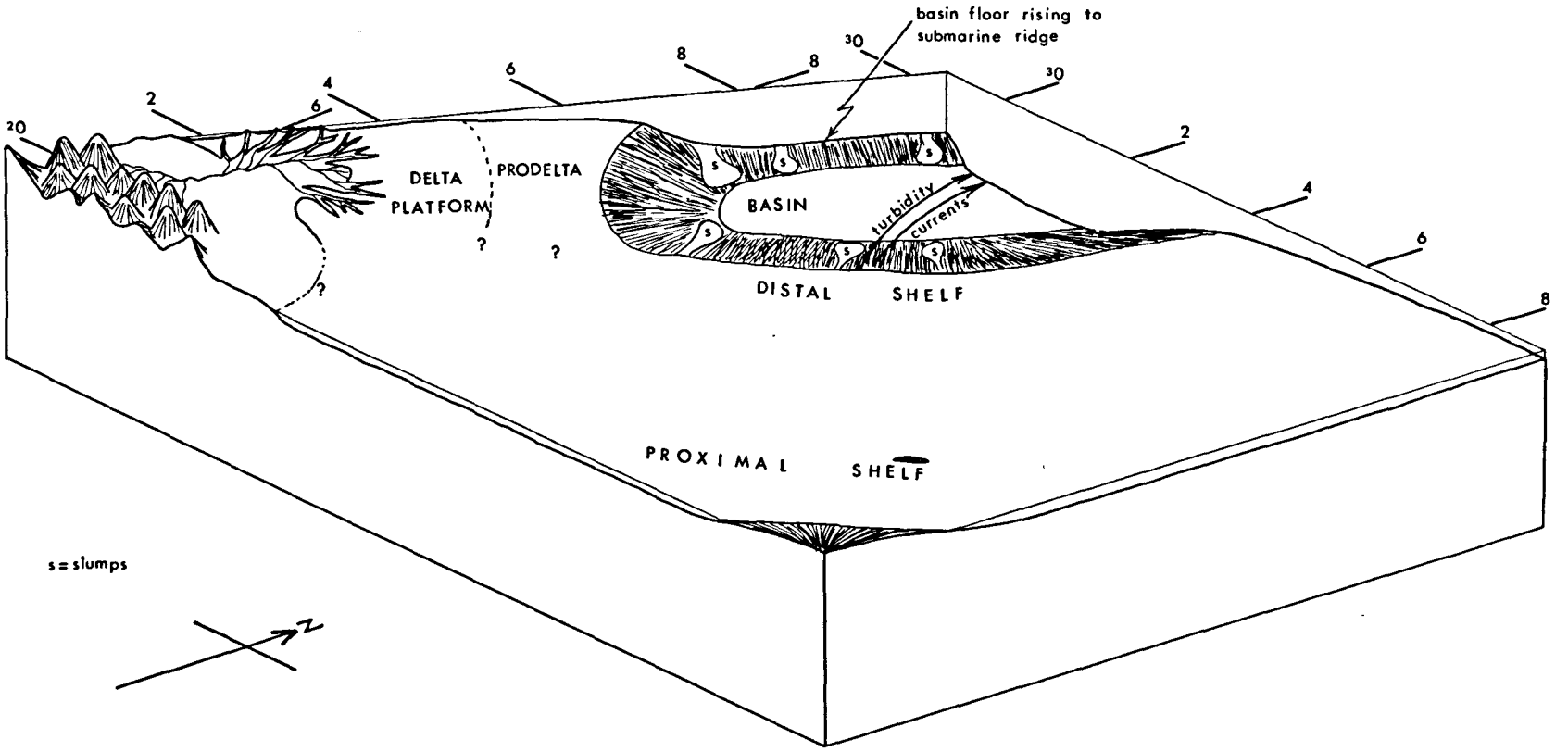

Fig. 6.1 Reconstruction of lower Bringewoodian palaeogeography. National Grid shown.

of the Lower Bringewoodian belonged to one community or assemblage, implying it was fairly homogeneous both laterally and vertically throughout the shelf strata of this unit. No previous palaeoecological collections had been made from the lower Bringewoodian of the basin or Llandovery-Llandeilo areas.

By comprehensively examining and quantitatively recording the faunal distribution in the lower Bringewoodian of Wales and the Welsh Borderland it has been shown that considerable lateral and vertical changes in faunal composition occur within this unit. The suggestion of a homogeneous faunal assemblage for the whole shelf lower Bringewoodian is a huge oversimplification.

It is considered vital to recognise transported assemblages, as a sample from them may give a totally erroneous impression not just of the abundance of a species but of its presence as a once live member of the fauna in the area being studied.

FACTORS CONTROLLING FAUNAL DISTRIBUTION

Having distinguished transported and untransported faunas it was possible to explain the occurrence and abundance of species using data on the palaeoenvironment, as derived from sedimentological studies, and the autecology of each form, as derived from studies of functional morphology. It was concluded that a species was, predictably, most abundant in the physical environment to which it was best adapted.

The distribution of the fauna in the strata examined in this study appears to have been controlled by a complex of physical environmental parameters; such as variations in turbulence and or wave buffeting, shifting of substrates due to reworking (physical and biological), sedimentation rates, turbidity, substrate type, salinity variations, temperature and exposure fluctuations and oxygenation of bottom waters(and therefore nutrient supply). Various combinations of these factors exerted influence in each of the lower Bringewoodian environments identified in this study.

The proposal by Calef & Hancock (1974) and Fürsich & Hurst (1974) that variation in food supply with depth was the major control on Ludlovian faunal distribution is rejected for many reasons (e.g. p.91, 92) including the one that suggests it is unlikely to have been a limiting factor in epeiric seas (Hallam 1965; Rhoads 1975). This study has shown that a whole complex of physical environmental factors, which may vary independently of depth, was responsible for controlling the faunal distribution at this level.

Changes in the physical environment influenced the quantitative and qualitative characteristics of faunal assemblages. As conditions became limiting for individual species they were excluded or became rare, while other species better adapted for the new environment entered the fauna and or noticeably increased in abundance. Species appear to occur together only where their environmental tolerances overlap. A large degree of species independence apparently therefore existed although predators must have been limited by the distribution of their prey. Other researchers in the British Silurian have also stressed the importance of physical environmental control on faunas e.g. Ziegler (1965), Ziegler et al. (1968), Watkins (1975, 1979), Cherns (1977).

The above conclusions confirm the arguments of Johnson (1964, p.129) that "benthic communities are commonly associates of largely independent species occurring together because of similar responses to the physical environment." Johnson (1964, p.129) further argued that this independence would be advantageous for individual species since it enables them to be highly adaptive.

As Thayer (1974) notes, physical (rather than biotic) control was far more likely in the Palaeozoic since taxa had yet to become specialised for occupying narrowly divided niches (Valentine 1969) a condition which involves increased competition between taxa. Therefore the marked influence of physical factors on the composition of lower Bringewoodian faunas is consistent with what is known of the evolution of marine communities.

Changes in faunal diversity and density values in different lower Bringewoodian environments can be related to the degree of physiological stress exerted by each environment. The highest stress conditions produced the lowest density and diversity values (e.g. the parallel laminated flags were deposited in the most stressful environment examined in this study and accordingly have the lowest density and diversity values. Such a relationship is well documented in modern work (p. 95).

The discreteness and number of lower Bringewoodian assemblages is a product of the environmental history at this time. There appear to have been extensive periods and areas over which the environment, and therefore fauna, was fairly constant. Between these periods or areas rapid environmental changes took place resulting in a new faunal assemblage rapidly replacing the former in the new environment, e.g. the change from the outer shelf bioturbated siltstone facies to the basin parallel laminated flags involves the replacement of shelf assemblage 1 with

the radically different basin assemblage 1 fauna. However, not all boundaries between environments were sharp and some gradual environmental gradients existed too, e.g. the environmental gradient in the bioturbated siltstone facies which produced a faunal gradient between inner and outer shelf. These observations support Johnson's (1972) proposal that faunal gradients reflect environmental gradients. Again, work on modern faunas has also supported this hypothesis (p. 95) which further suggests the strong control by the physical environment on the fauna.

CONCLUSION

Only by using sampling techniques which give a complete and representative picture of the fauna as well as stratigraphical and sedimentological techniques which permit the recognition of transported assemblages and the effective reconstruction of ancient environments, can fossil assemblages be meaningfully studied in terms of palaeoecology. Failure to observe any of these points may lead to erroneous palaeoecological conclusions.

The necessity of examining faunas in terms of an environmental framework, established independently of faunal information, is stressed. Failure to do this in the past (e.g. Calef & Hancock 1974) has hindered progress on Ludlow palaeoecology.

APPENDIX I

RAW DATA

Raw data - number of individual fossils of each taxa in each collection, together with density and diversity data for all 17 localities visited, in the order they are referred to in the text (i.e. Aymestrey, Leintwardine, River Onny, Ludlow, Millichope, Woodbury, Perton Lane, Usk, Brookend borehole, Knill, Knighton, Kerry, Builth Wells, Cwm Graig Ddû, Gwydderig, Sawdde and Cennen).

NUMBER OF INDIVIDUALS	=	number of individual fossils identified in each collection.
DENSITY PER 5000 cm^3	=	number of individuals per 5000 cm^3 of sediment.
NUMBER OF SPECIES	=	number of species per collection.
DIVERSITY PER 100 INDIV.	=	number of species per 100 individuals.

Raw Data – Aymestrey

	A31	A30	A29	A28	A25	A27	A24	A26	A23	A24	A23	A22	A21	A20	A19	A18	A17	A16	A15	A14	A13	A12	A11	A10	A9	A8	A7	A6	A5	A4	A3	A2	A1
A. grayi	-	-	-	-	-	-	1	1	7	5	1	1	1	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
A. fimbriata	2	1	-	-	1	-	2	1	1	1	2	1	2	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
A. reticulata	13	1	25	7	2	18	3	2	2	7	2	2	1	2	1	1	1	1	1	1	1	7	3	1	3	4	2	1	1	1	1	1	1
C. implicata	-	1	3	1	1	3	1	1	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
dalmanellids indet.	1	3	5	5	17	1	9	1	2	2	5	21	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
D. navicula	1	1	1	1	1	1	1	3	6	3	1	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
R. radiatus	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
G. lata	2	1	1	4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
H. elegans	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
I. orbicularis	2	1	1	1	6	22	28	3	9	2	1	15	17	3	1	1	1	1	1	1	1	1	1	1	6	1	20	1	1	1	1	1	1
K. knighti	1	93	5	4	6	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
L. depressa	5	1	3	1	3	1	1	1	1	1	5	11	1	1	4	2	2	1	2	1	1	6	3	1	1	1	4	1	1	1	1	1	1
L. filosa	1	1	1	1	1	12	5	3	1	5	16	2	2	1	1	1	1	1	2	1	1	1	1	1	5	1	1	1	1	1	1	1	1
L. lata	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
L. levisli	1	1	1	1	1	1	1	1	3	1	2	1	1	1	1	1	1	1	4	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M. cf. lepisma	1	1	1	1	1	2	9	3	1	3	9	2	1	1	1	1	1	2	1	2	1	5	3	1	6	1	1	1	1	1	1	1	1
M. nucula	1	1	1	1	1	1	1	4	1	1	3	1	1	1	1	1	1	1	2	1	1	3	1	1	3	1	1	1	1	1	1	1	1
P. minima	1	1	1	1	1	1	1	2	1	4	1	3	2	1	2	1	1	1	2	1	1	4	2	1	3	1	2	1	1	1	1	1	1
S. ludlovensis	4	1	3	1	3	62	157	3	597	106	2	533	452	4	489	716	3	361	132	1	192	2	66	118	73	140	91	76	21	2	73	108	57	44	265	1	83	145	3	218	129	231	1	49	110	281	122
Shaleria sp. nov.	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
S. euglypha	1	1	2	13	2	15	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1
S. wilsoni	1	1	2	2	15	1	1	1	1	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
A. plewroptera	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
C. planulata	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
C. subplanulata	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
L. reticulata	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M. antiquus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
O. nasuta	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
bivalve indet.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Calymene sp.	1	1	17	13	31	4	18	22	10	6	21	3	1	6	4	1	2	1	1	2	6	8	4	3	2	1	2	10	1	1	1	1	6	1	1	1	1	1	1	1	1	1	1	1	1	1	1
D. myope	9	1	17	13	31	4	18	22	10	6	21	3	1	6	4	1	2	1	1	2	6	8	4	3	2	1	2	10	1	1	1	1	6	1	1	1	1	1	1	1	1	1	1	1	1	1	1
P. obconicus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	25	6	2	146	6	1	7	5	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
beyrichiaceans	2	1	3	1	1	1	1	1	6	1	3	1	3	1	1	1	1	1	1	1	4	1	1	1	25	25	18	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
smooth ostracods	12	1	4	1	11	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ceramopora sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
dendroid trepostome	1	1	2	1	1	2	1	2	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
encrusting trepostome	1	1	3	1	4	2	1	1	2	3	4	1	2	1	1	1	1	1	1	1	1	3	6	1	1	6	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Fistulipora sp.	1	1	3	3	4	15	10	1	2	14	1	10	1	7	1	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
P. lanceolata	1	1	1	6	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
vinculariiform trepostome	1	1	7	3	10	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
L. striatissima	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
L. obsoletum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
P. globosa	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Polemnita sp. nov.	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Favosites sp.	4	1	1	6	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
R. porpitoides	4	1	1	6	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
solitary coral sp. B	5	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Syringopora sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
'Cyrtoceras' sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
K. angulatum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
S.c. salweyi	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
T. ornatus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tentaculites sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
crinoid ossicles (round)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

	NUMBER OF INDIVIDUALS	NUMBER OF SPECIES	DIVERSITY PER 100 INDIV.
	79	23	-
	95	7	-
	78	17	-
	61	17	-
	18	6	-
	133	18	17.0
	77	5	-
	224	12	8.2
	703	15	8.5
	133	13	11.8
	591	14	7.8
	478	16	6.0
	537	19	9.8
	814	16	9.5
	446	13	9.6
	144	9	7.5
	216	10	7.4
	77	7	-
	126	8	6.8
	80	8	-
	153	9	8.1
	96	5	-
	87	9	-
	24	3	-
	112	15	14.5
	141	14	12.2
	70	7	-
	55	6	-
	428	17	10.8
	110	13	12.3
	221	17	12.9
	296	12	8.9
	151	3	2.6
	242	6	4.0
	52	4	-
	111	2	1.9
	304	8	5.2
	190	4	3.8

	T18	T46	T47	T45	T43	T42	T41	T40	T39	T38	T37	T36	T35	T34	T33	T32	T31	T30	T29	T28	T27	T26	T25	T24	T23	T22	T21	T20	T19	T18	T17	T16	T15	T14	T13	T12	T11	T10	T9	T8	T7	T6	T5	T4	T3	T2	T1
A.gray1																																																
A.funiculata																																																
A.reticularia	30	28	21	8	12	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	11	12	10	10	10	10	10	10	10	12	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
C.pecten																																																
C.leptiformis																																																
Calmanellida indet.	2																																															
small dalmanellid																																																
Eradiatus																																																
G.galeata																																																
G.lata	2																																																
H.elegans																																																
I.orbicularis																																																
K.knightii																																																
L.depressa																																																
L.fillosa																																																
L.lata																																																
L.levisii																																																
Lingula sp. A																																																
M.cf.lepidum																																																
O.rugata																																																
P.minimus																																																
S.ludloviensis	17	55	84	145	167	303	174	67	70	115	92	96	63	67	105	81	83	107	137	78	88	51	49	53	75	98	75	96	75	68	68	39	71	55	29	56	85	70	76	98	93	72	44	48	28	30	
Shalerta sp. nov.																																																
S.vilasoni																																																
S.eugiypha	52	15																																														
A.plesuropterа																																																
C.cornucopiae																																																
C.planulata																																																
G.cymbaeformis																																																
Hodiolopsis sp.																																																
N.antiquus																																																
?Parracyclus																																																
P.tenuistriata																																																
bivalve indet.																																																
D.wygope																																																
Howlargoe sp.																																																
P.obconicus																																																
beyrichiaceans																																																
smooth ostracods																																																
Ceramopora sp.																																																
dendroid treposome																																																
encrusting treposome																																																
Fistulipora sp.																																																
P.lanceolata																																																
Vinculariiform treposome	14					10																																									
B.lloydii																																																
L.atlantisensa																																																
L.obsoletum																																																
P.globosa																																																
Favosites sp.																																																
R.porpitoides																																																
small horn corals																																																
solitary coral sp. A																																																
solitary coral sp. B																																																
Cyrtoceras sp.																																																
D.nicholsanum																																																
K.angulatum																																																
K.bullatum																																																
O.subundulatum																																																
P.ibex																																																
P.tumescens																																																
S.clunensis																																																
S.incipiens																																																
T.ornatus																																																
crinoid ossicles (round)																																																

	NUMBER OF INDIVIDUALS	DENSITY PER 2000 cm³	NUMBER OF SPECIES	DIVERSITY PER 100 INDIV.
T18	101	13.5	14	14.0
T46	112	23.3	17	16.6
T47	106	22.3	17	16.2
T45	112	23.3	10	10.5
T43	178	37.0	10	8.4
T42	114	23.8	11	10.5
T41	329	3650.0	8	5.1
T40	214	44.6	12	9.1
T39	111	23.1	15	14.4
T38	101	21.0	13	13.0
T37	101	21.0	17	17.0
T36	149	31.0	15	11.1
T35	135	28.1	14	11.0
T34	109	22.7	15	14.2
T33	110	22.9	19	17.0
T32	130	27.1	17	15.2
T31	102	21.3	12	12.0
T30	117	24.4	15	14.0
T29	146	30.4	17	14.9
T28	149	31.0	9	7.5
T27	103	21.3	12	12.0
T26	104	21.7	11	11.0
T25	107	16.5	8	7.0
T24	107	16.5	12	11.1
T23	106	22.1	15	14.1
T22	102	21.3	16	15.0
T21	131	27.3	15	11.2
T20	104	21.7	11	11.0
T19	108	22.9	17	15.9
T18	107	22.3	17	15.5
T17	105	21.9	20	20.0
T16	104	21.7	18	16.0
T15	100	20.7	20	19.1
T14	113	23.6	12	9.9
T13	121	25.6	18	16.4
T12	121	25.8	23	34.4
T11	106	22.1	13	12.1
T10	106	22.1	18	17.2
T9	211	44.0	21	15.1
T8	124	25.8	13	11.8
T7	128	26.7	19	17.6
T6	101	21.0	19	19.0
T5	100	20.8	17	17.0
T4	105	14.9	15	15.0
T3	119	12.2	15	17.2
T2				
T1				

Raw Data - Leintwardine

Raw Data - River Onny

| SITE | A.gryi | A.funiculata | A.reticularia | C.pecten | C.implicata | dalmanellida indet. | small dalmanellid | G.lata | H.elegans | I.orbicularis | K.knighti | L.depressa | L.filosa | L.lata | L.levisli | M.cf.lepisma | P.minima | S.ludloviensis | Shaleria sp. nov. | S.Wilsoni | S.euglypha | C.cornucopiae | C.planulata | C.subplanulata | G.cymbeformis | L.reticulata | N.antiquus | O.nasuta | bivalve indet. | D.wygoe | E.rosenstelnae | P.obconicus | beyrichiacean | smooth ostracods | Ceramopora sp. | dendroid trepostome | encrusting trepostome | Fistulipora sp. | F.lanceolata | Vinculariiform trepostome | B.Ilaydii | L.bifurcatisima | L.obsoletum | P.globosa | Favosites sp. | R.porpitoides | small horn corals | solitary coral sp. B | Cyrtocrina sp. | h.angulatum | ?O.subundulatum | P.tumescens | T.ornatus | crinoid ossicles (round) | NUMBER OF INDIVIDUALS | DENSITY PER 5000 cm^3 | NUMBER OF SPECIES | DIVERSITY PER 100 INDIV. |
|---|---|---

Raw Data - Ludlow

Raw Data - Millichope

	A.grayi	A.funiculata	A.reticularis	C.implicata	dulmanellids indet.	E.radiatus	G.galeata	G.lata	H.elegans	I.orbicularis	L.depressa	L.filosa	L.lewisii	M.cf.lepisma	P.ludloviensis	P.minimus	S.ludloviensis	Shaleria sp. nov.	S.wilsoni	S.euglypha	A.pleuroptera	C.planulata	C.subplanulata	G.cymbaeformis	O.nasuta	P.mytilimeris	D.myops	E.rosensteinae	P.astringens	beyrichiaceans	smooth ostracods	Ceramopora sp.	dendroid trepostome	encrusting trepostome	Fistulipora sp.	P.lanceolata	vinculariiform trepostome	L.striatissima	P.globosa	Favosites sp.	small horn corals	solitary coral sp. B	Syringopora sp.	K.angulatum	P.ibex	S.chimaera s.l.	crinoid ossicles (round)	NUMBER OF INDIVIDUALS	DENSITY PER 5000 cm^3	NUMBER OF SPECIES	DIVERSITY PER 100 INDIV.
LUB	-	-	32	3	2	-	-	19	3	13	-	-	-	-	-	-	-	-	13	8	-	-	-	-	-	-	3	-	-	-	4	-	5	-	3	1	1	-	1	-	-	-	-	-	1	1	124	45.9	17	16.6
M21	-	-	6	1	-	-	-	13	-	4	-	25	-	26	-	-	6	-	4	4	-	-	1	-	-	-	-	-	-	-	1	-	-	-	1	1	-	-	1	-	-	-	-	-	1	1	102	72.3	17	17.0
M20	-	-	7	-	-	-	-	13	-	20	4	13	-	24	-	1	4	-	2	-	-	-	-	-	-	-	4	-	-	-	-	-	-	2	3	1	-	-	1	-	-	-	-	-	1	1	103	643.8	16	16.0
M19	-	15	4	-	-	-	-	29	-	4	2	12	1	48	-	-	7	-	3	6	-	-	-	-	-	-	-	-	-	-	3	-	-	-	2	3	1	1	-	-	-	1	-	-	-	-	141	125.3	16	14.8
M18	1	24	2	1	3	-	-	16	-	3	17	25	-	42	-	4	10	-	5	13	-	-	-	-	-	-	1	-	-	-	3	-	-	-	1	3	-	-	-	-	-	-	-	-	-	-	185	1027.8	20	17.0
M17	-	10	-	-	1	-	-	16	-	3	1	9	-	50	-	-	7	1	3	8	-	-	-	-	-	-	-	-	1	-	1	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	119	208.8	17	15.8
M16	2	8	3	-	-	-	-	28	-	4	-	-	-	66	-	-	4	-	4	-	-	-	-	-	-	-	-	1	1	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	128	853.3	13	12.4
M15	1	4	9	-	-	-	1	18	2	3	-	-	-	51	-	-	8	1	3	10	-	-	-	-	-	1	-	-	-	1	4	-	-	1	2	2	-	-	-	-	-	-	-	-	-	-	129	195.5	21	18.9
M14	-	1	2	-	-	-	-	14	-	4	1	1	-	53	-	-	2	-	-	16	-	-	-	-	-	-	-	-	-	-	-	12	-	-	4	4	-	-	-	-	-	-	-	-	-	-	105	875.0	13	13.0
M13	1	6	5	-	-	-	-	20	-	2	-	3	1	46	-	-	9	-	3	12	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	133	107.3	20	18.8
M12	3	21	5	-	-	-	-	16	-	10	4	-	1	20	1	-	13	-	8	17	-	-	-	-	-	-	-	-	-	-	1	-	-	-	3	1	11	-	-	-	-	-	-	-	-	-	-	160	121.2	20	18.0
M11	-	16	-	-	-	-	-	7	-	13	2	-	-	19	-	1	3	-	21	9	-	-	-	-	-	-	-	-	-	-	6	-	-	-	1	5	-	4	-	3	-	-	-	-	-	-	112	933.3	16	15.6
M10	3	4	7	-	-	-	-	6	-	4	1	3	1	31	-	3	20	-	2	3	-	-	1	-	-	-	-	1	-	-	1	1	1	-	-	2	-	12	-	-	1	2	-	-	1	-	-	112	73.7	24	23.0
M 9	1	14	-	-	-	-	-	9	-	14	1	-	-	38	-	1	17	-	-	2	-	-	-	-	-	-	-	4	2	1	-	8	-	-	-	-	1	-	-	-	-	-	-	-	-	-	114	950.0	15	14.4
M 8	-	9	1	-	-	-	-	11	-	3	-	4	3	33	-	-	21	1	3	2	-	-	-	-	-	-	-	1	-	-	-	5	-	-	-	2	-	5	-	1	-	-	1	-	-	-	102	45.5	17	17.0
M 7	-	5	-	-	-	-	-	-	-	6	-	11	-	48	3	1	13	-	2	6	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	4	-	4	-	-	-	-	-	-	-	-	111	693.8	14	13.8
M 6	-	8	4	2	-	-	-	5	-	7	-	20	1	26	-	-	1	1	4	1	-	-	1	-	-	-	-	2	1	1	1	4	3	-	-	1	3	-	9	-	4	-	1	1	-	-	-	125	109.6	26	23.6
M 5	-	22	1	-	-	-	-	-	-	5	-	22	-	9	-	-	22	-	-	4	-	-	-	-	-	-	-	1	-	1	-	9	-	-	-	1	-	4	-	-	-	-	-	-	-	-	102	637.5	13	13.0
M 4	-	20	1	-	-	-	-	-	-	11	-	-	-	20	1	1	20	1	5	3	1	-	-	-	-	-	-	3	-	1	-	4	-	-	-	4	-	8	-	-	-	-	-	-	-	-	124	151.2	13	12.8
M 3	-	50	-	-	-	-	-	2	-	-	-	2	1	11	-	-	13	-	8	9	-	-	-	1	1	-	-	-	1	-	-	1	-	-	-	-	-	4	-	-	-	-	-	-	-	-	108	42.5	15	14.4
M 2	-	39	-	-	-	-	-	-	-	18	-	-	-	4	-	-	6	-	25	3	-	-	-	-	-	-	-	1	-	-	-	2	-	-	-	-	1	2	-	-	-	-	-	-	-	1	102	1275.0	11	11.0
M 1	-	27	3	-	-	-	4	-	-	6	1	4	2	10	-	-	26	-	4	3	1	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	4	-	-	1	3	-	-	-	1	-	102	32.7	18	18.0

A. fallaciosa
A. rotaliaria
B. perlata
C. impolita
Salmacellina index.
E. radiosa
F. glabrata
G. lata
H. elegans
I. ovalaeformis
J. lepreosa
K. filosa
L. levicula
M. cf. japigna
N. scutula
O. rugosa
P. laticostata
P. minima
S. laticostata
Bolivina sp. nov.
T. vitrea?
U. quadrata
A. plumosoria
C. plumosa
C. ampliamulata
L. reticulata
Pseudotaxilla sp.
Reticulotaxilla sp.
Bolivina index.
Cassyna sp.
B. spp?
E. rosacostata
F. serrulata
Hyrrokkinidae
Quinqueloculina sp.
Amphicoryna scalaris
Amphimorphina haueriana
Ammonia beccarii tepidaeformis
Elphidium sp.
Pseudononion atlanticum
Pyrgo depressa
Pyrgoella sp.
Quinqueloculina sp.
Spiroloculina sp.
Triloculina sp.
Triloculina trigonula
Triloculina tricarinata
Triloculina index.
Miliolinella subrotunda
Miliolinella labiosa
Miliolinella circularis (round)
Miliolinella subcircularis
Miliolinella inflata
Miliolinella webbiana
Miliolinella sp. A
Miliolinella sp. B
Miliolinella subfabaginea
Miliolinella subrotunda (round)
Miliolinella labiosa (round)
Miliolinella circularis (round)
NUMBER OF INDIVIDUALS
NUMBER PER 5000 cm³
NUMBER OF SPECIES
DIVERSITY PER 100 INDIV.

146	81.1	19.0	16.9
101	673.3	10.0	10.0
135	82.3	17.0	15.2
103	686.7	11.0	11.0
127	69.8	14.0	12.8
215	1433.3	14.0	10.5
110	74.3	14.0	13.3
184	2300.0	3.0	3.0
114	95.0	13.0	12.9
105	87.5	15.0	15.0
149	993.3	12.0	10.8
106	62.4	15.0	14.4
252	1680.0	12.0	9.0
107	62.2	12.0	11.6
173	1153.3	10.0	9.6
109	71.7	18.0	16.9
212	883.3	15.0	11.8
167	91.8	14.0	12.4
396	1650.0	16.0	10.9
114	82.6	15.0	14.7
172	1433.3	19.0	17.4
156	109.9	13.0	12.2
240	1600.0	18.0	14.0
220	1833.3	20.0	16.2
135	132.4	13.0	10.9
237	1481.3	12.0	9.6
125	104.2	18.0	16.2
172	1075.0	15.0	14.2
154	95.1	19.0	16.2
121	100.8	16.0	15.0
104	86.7	12.0	12.0
169	1126.7	16.0	14.4
130	71.4	16.0	14.8
175	1166.7	13.0	11.4
111	84.1	16.0	15.5
112	93.3	15.0	14.6
105	585.3	8.0	8.0
150	93.8	16.0	14.2
284	1781.3	17.0	11.3
144	79.1	15.0	14.1
145	966.7	10.0	8.8
105	875.0	5.0	5.0
117	74.1	15.0	14.9
321	1337.5	16.0	12.6
110	91.7	17.0	16.9
102	850.0	15.0	15.0
103	85.8	18.0	18.0
109	76.8	18.0	17.1
103	858.3	17.0	17.0
108	90.0	14.0	13.4
119	793.3	14.0	13.2
118	98.3	12.0	11.2
350	1458.3	21.0	15.9
134	84.8	15.0	13.8
186	1240.0	12.0	11.0
156	1733.3	16.0	14.4
127	124.5	19.0	17.4
107	713.3	14.0	13.8
99	110.0	14.0	14.0
104	693.3	14.0	14.0
102	118.6	25.0	25.0
108	163.6	18.0	17.4

Raw Data - Woodbury

	P26	P25	P24	P23	P22	P21	P20	P19	P18	P17	P16	P15	P14	P13	P12	P11	P10	P9	P8	P7	P6	P5	P4	P3	P2	P1
A.fumeulata	1	1	1	4	2	2	1	1	1	1	2	4	1	1	1	1	4	2	2	1	1	1	1	1	1	1
A.reticularis	44	38	45	50	57	45	59	30	27	20	21	21	2	19	7	44	6	48	47	25	16	11	27	15	1	
C.implicata	1	3	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
dalmanellids indet.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
E.radiatus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
G.galeata	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
G.lata	2	3	2	2	3	2	1	1	1	2	2	2	2	2	1	1	1	1	2	3	2	2	3	2	1	
H.elegans	1	2	1	1	1	1	1	1	1	2	2	1	1	1	1	2	2	1	1	1	2	1	1	1	1	
I.orbicularis	9	13	19	18	29	5	10	5	8	8	8	6	1	7	1	10	8	17	27	7	13	12	6	14	4	
K.knighti	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
L.depressa	2	1	1	3	3	1	4	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
L.filosa	1	1	1	2	1	2	1	1	1	1	1	1	1	58	4	1	1	2	2	2	11	1	1	1	1	
L.levisii	3	1	3	1	1	1	1	1	4	2	1	1	1	1	3	1	1	2	1	1	3	1	2	1	1	
M.cf.lepidus	1	1	1	6	10	3	6	2	1	1	19	12	16	15	2	9	10	9	13	8	16	15	25	14	16	1
M.nucula	1	1	1	1	1	1	1	2	1	3	1	2	1	1	1	1	1	1	1	1	1	1	1	2	1	
P.ludloviensis	1	3	1	1	1	2	1	1	1	1	1	2	1	2	1	2	1	1	1	1	1	3	1	2	1	
P.minimus	1	1	3	12	12	4	2	10	10	30	27	20	4	16	13	32	28	8	27	7	22	28	32	12	19	85
S.ludloviensis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Bhalerta sp. nov.	7	3	3	3	3	3	3	47	7	8	8	8	8	23	20	89	21	3	3	3	3	2	3	3	3	1
S.vilasoni	4	2	6	6	6	7	6	1	3	1	4	4	2	1	1	11	39	3	5	11	75	15	31	18	1	
S.euglypha	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
C.planiata	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
G.cymbaeformis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Gramysia sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
N.antiquus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	4	
O.nasuta	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
P.mytilimeria	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
bivalve indet.	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
D.wyope	1	1	1	3	1	1	2	1	1	2	2	2	1	1	1	1	1	3	3	3	3	2	2	1	1	
E.rosenstelnae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	
P.austringens	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
beyrichiacean	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	
smooth ostracods	4	5	4	13	11	8	10	1	1	4	1	1	1	1	1	1	33	4	1	1	11	2	5	1	1	
Ceramopora sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
dendroid trepostome	5	2	2	4	2	2	5	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
encrusting trepostome	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Fistulipora sp.	3	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	1	1	2	1	1	1	
P.lanceolata	1	1	3	1	4	1	1	1	2	2	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	
Vinculariiform trepostome	14	11	6	15	20	4	10	1	10	8	1	4	16	1	4	1	1	1	3	1	3	1	1	1	1	
L.atriatissima	1	1	1	1	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	
L.obsoletum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	
P.globosa	3	3	3	3	2	2	1	3	3	1	4	1	3	1	3	1	1	1	1	1	1	1	1	1	1	
Polemita sp. nov.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Favosites sp.	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
R.porpitoides	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
solitary coral sp. B	4	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Gomphoceras sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
K.angulatum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Q.subundulatum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	
P.tumescens	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	13	
S.chimera n.s.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Kellorites sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
T.ornatus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
crinoid ossicles (round)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	

Raw Data - Perton Lane

	A.grayi	A.funiculata	A.reticularis	C.implicata	dalmanellids indet.	E.radiatus	G.galeata	G.lata	H.elegans	I.orbiculatis	L.depressa	L.fiiloa	L.lovisii	M.cf.lepidus	M.nucula	P.ludloviensis	P.minimus	S.ludloviensis	Shaleria sp. nov.	S.villaoni	S.euglypha	C.planulata	L.reticulata	N.antiquus	O.nasuta	bivalve indet.	D.wygae	E.rosenstelnae	F.astringens	beyrichiacems	smooth ostracods	Cermopora sp.	dendroid trepostome	encrusting trepostome	Fistulipora sp.	P.lanceolata	Vinculariiform trepostome	L.striatissima	L.obsoletum	P.globosa	Polesmita sp. nov.	Favosites sp.	R.porpitoides	solitary coral sp. B	K.angulatum	M.bullatum	Graptolite indet.	T.ornatus	crinoid ossicles (round)	NUMBER OF INDIVIDUALS	DENSITY PER 5000 cm^3	NUMBER OF SPECIES	DIVERSITY PER 100 INDIV.
U22	2	87	26	1	1	1	1	1	1	9	7	18	1	22	1	3	1	1	8	3	1	14	30	1	1	1	1	5	1	1	1	3	1	1	5	4	10	16	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	165	91.7	14	12.4
U21	1	1	70	1	1	1	1	1	11	7	1	6	1	10	1	1	1	1	3	2	1	1	11	16	2	10	3	1	1	1	1	2	1	1	1	1	16	12	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	138	107.8	18	16.2
U20	1	1	66	1	1	1	1	1	2	11	5	8	1	10	1	1	1	1	8	1	1	1	10	7	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	144	960.0	16	15.4
U19	1	3	59	1	1	2	1	1	8	21	13	13	1	3	1	1	1	1	3	1	1	1	7	12	1	24	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	168	118.3	19	17.0
U18	1	4	64	1	1	1	1	1	11	9	3	14	1	24	1	1	1	1	10	1	1	1	12	8	1	2	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	153	850.0	15	14.7
U17	1	5	82	1	1	2	1	1	8	9	2	6	1	11	1	1	1	1	3	1	1	1	8	6	1	2	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	178	148.3	17	16.6
U16	1	6	80	1	1	1	1	1	8	8	2	31	1	5	1	1	1	1	12	1	1	1	10	7	1	2	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	142	1183.3	16	15.4
U15	1	1	52	1	1	1	1	1	1	2	2	28	1	28	1	1	1	1	6	1	1	1	23	9	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	202	202.0	16	15.0
U14	1	1	65	1	1	1	1	1	1	10	1	9	1	9	1	1	1	1	16	1	1	1	10	9	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	124	1033.3	10	9.6
U13	1	1	77	1	1	1	1	1	1	7	1	9	1	4	1	1	1	1	3	1	1	1	5	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	173	135.2	18	16.0
U12	1	1	45	1	1	1	1	1	1	4	1	6	1	2	1	1	1	1	6	1	1	1	10	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	118	786.7	10	9.4
U11	1	1	23	1	1	1	1	1	3	11	1	2	1	24	1	1	1	1	16	1	1	1	5	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	101	101.0	17	17.0
U10	1	1	11	1	1	1	1	1	1	4	1	2	1	14	1	1	1	1	5	1	1	1	6	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	157	151.0	25	20.6
U9	1	1	14	1	1	1	1	1	3	16	1	4	1	26	1	1	1	1	21	1	1	1	7	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	108	900.0	15	14.8
U8	1	1	29	1	1	1	1	1	2	13	1	4	1	7	1	1	1	1	21	1	1	1	10	4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	162	126.6	25	22.6
U7	1	1	34	1	1	1	1	1	1	7	1	4	1	26	1	1	1	1	21	1	1	1	9	4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	114	950.0	14	13.5
U6	1	1	28	1	1	1	1	1	2	13	1	4	1	7	1	1	1	1	21	1	1	1	9	4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	163	121.6	21	18.2
U5	1	1	28	1	1	1	1	1	2	20	1	6	1	18	1	1	1	1	12	1	1	1	38	10	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	158	1170.4	16	15.6
U4	1	1	37	1	1	1	1	1	2	19	1	6	1	12	1	1	1	1	12	1	1	1	33	10	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	156	130.0	18	15.6
U3	1	2	33	1	1	1	1	1	1	19	1	2	1	30	1	1	1	1	31	1	1	1	13	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	174	160.0	13	12.2
U2	1	3	28	1	1	1	1	1	1	4	1	7	1	12	1	1	1	1	1	1	1	1	28	4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	187	157.5	20	17.5
U1	1	3	26	1	1	1	1	1	1	2	1	9	1	22	1	1	1	1	14	1	1	1	34	14	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	124	1033.3	14	13.6
U0	2	1	1	1	1	1	1	2	1	14	1	1	1	3	1	2	1	1	74	1	1	1	9	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	175	134.6	21	19.4
U0E	2	1	1	1	1	1	1	1	1	6	1	1	1	1	1	2	1	1	6	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	117	24.4	16	15.1

Raw Data - Usk

Raw Data – Brookend borehole

Raw Data - Knill

	A. gryi	dalmanellids indet.	D. navicula	I. orbicularis	L. depressa	L. lata	M. cf. lepisma	M. nucula	P. minimus	S. ludloviensis	S. wilsoni	C. cornucopiae	P. tenuistriata	C. cf. lawsoni	D. myops	E. rosensteinae	E. stubblefieldi	P. obconicus	beyrichiaceans	smooth ostracods	encrusting trepostome	K. angulatum	'O'. dimidiatum	'O'. subundulatum	P. ibex	graptolites	S.c. semispinosus	S. incipiens	S. varians subsp. nov.	crinoid ossicles (round)	crinoid ossicles (pentagonal)	NUMBER OF INDIVIDUALS	DENSITY PER 5000 cm^3	NUMBER OF SPECIES	DIVERSITY PER 100 INDIV.
K16S3	23	-	6	-	-	1	-	-	1	1	-	-	-	-	-	2	-	-	32	-	1	-	-	-	-	-	-	-	-	1	66	6600.0	8.0	-
K16S2	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	25	-	5	-	-	-	-	-	-	-	-	-	1	68	6800.0	7.0	-
K16S1	18	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	9	-	-	-	-	-	-	-	-	-	-	-	1	31	3100.0	4.0	-
K16	2	-	-	-	-	2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	3	3	2	-	-	-	-	-	13	0.5	6.0	-
K15	-	-	31	7	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-	2	-	-	1	1	-	-	-	-	-	-	45	7.5	7.0	-
K14	-	-	-	-	-	5	-	-	-	-	1	3	-	-	-	-	-	-	-	-	-	-	12	4	-	-	-	-	-	-	25	1.0	5.0	-
K13	-	-	-	-	-	5	-	-	-	-	-	8	-	-	-	-	-	-	-	-	-	1	24	3	1	-	-	-	-	-	42	1.8	6.0	-
K12	20	-	10	1	-	-	-	-	-	2	1	-	-	-	6	-	-	-	4	8	-	-	-	5	-	-	-	-	-	-	57	9.5	9.0	-
K11S1	21	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	11	7	-	-	-	-	-	-	-	-	-	-	-	41	4100.0	4.0	-
K11	3	-	-	-	-	2	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	1	18	-	9	-	-	-	-	35	1.5	6.0	-
K10G1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	52	-	-	-	-	52	5200.0	1.0	-
K10S2	112	-	-	-	-	3	-	-	-	3	-	-	-	-	-	-	-	1	5	-	-	-	-	-	-	-	-	-	-	1	125	6200.0	6.0	5.6
K10S1	118	-	-	-	-	4	-	-	-	6	-	-	-	-	-	-	-	2	5	-	-	-	1	3	-	-	-	-	-	-	149	7500.0	7.0	6.6
K10	4	-	-	-	-	7	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	18	-	47	-	x	-	-	78	3.3	5.0	-
K9S1	420	-	-	-	2	12	-	1	14	116	1	-	-	-	-	-	1	27	32	17	-	-	-	-	-	-	-	-	-	-	643	8000.0	11.0	7.9
K9	1	-	-	-	-	7	-	-	-	-	-	2	2	-	-	-	-	-	-	-	-	-	1	16	-	11	-	x	-	-	40	1.7	7.0	-
K8S1	398	2	-	-	-	12	-	-	-	41	1	-	-	-	-	-	1	3	4	14	-	-	-	-	-	-	-	-	-	-	476	6000.0	9.0	6.2
K8	1	-	-	-	-	8	-	-	-	-	2	4	1	-	-	-	-	-	-	-	-	-	2	52	-	14	-	-	-	-	84	3.5	8.0	-
K7	-	-	-	-	-	8	-	-	-	-	1	6	10	-	-	-	-	-	-	-	-	-	-	65	-	12	-	-	-	-	102	4.3	6.0	-
K6S1	-	-	-	2	-	4	-	1	-	40	14	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	64	6400.0	6.0	-
K6G1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	52	-	-	-	-	52	5200.0	1.0	-
K6P1	-	-	-	-	-	-	-	-	-	-	-	-	33	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	33	3300.0	1.0	-
K6	-	-	-	-	-	8	-	-	-	-	-	2	10	-	-	-	-	-	-	-	-	-	1	39	-	58	x	x	x	-	118	4.9	8.0	7.8
K5G1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	78	-	x	-	-	78	7800.0	1.0	-
K5S1	12	1	-	-	-	-	1	-	-	27	-	-	-	-	-	-	-	1	2	-	-	-	-	6	-	-	-	-	-	-	50	5000.0	7.0	-
K5P1	-	-	-	-	-	-	-	-	-	-	-	-	84	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	84	4200.0	1.0	-
K5	-	-	-	-	-	-	-	-	-	-	1	3	14	-	-	-	-	-	-	-	-	-	2	42	-	38	-	x	x	-	100	4.2	7.0	7.0
K4	-	-	-	-	-	4	-	-	-	54	-	-	-	-	-	-	-	-	-	-	-	-	1	25	-	-	-	-	-	-	84	14.2	4.0	-
K3P1	-	-	-	-	-	-	-	-	-	-	-	-	28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28	2800.0	1.0	-
K3	-	-	-	-	-	8	-	-	-	-	1	4	12	-	-	-	-	-	-	-	-	-	-	35	-	19	-	-	-	-	79	3.3	6.0	-
K2P3	-	-	-	-	-	-	-	-	-	-	-	-	68	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	68	3400.0	1.0	-
K2G3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	88	x	-	-	-	88	8800.0	1.0	-
K2P2	-	-	-	-	-	-	-	-	-	-	-	-	27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	27	2700.0	1.0	-
K2G2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	59	-	-	-	-	59	5900.0	1.0	-
K2P1	-	-	-	-	-	-	-	-	-	-	-	-	40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	40	4000.0	1.0	-
K2G1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	112	x	-	-	-	112	5600.0	1.0	1.0
K2	-	-	-	-	-	7	-	-	-	-	-	-	121	-	-	-	-	-	-	-	-	-	3	72	-	138	x	x	-	-	341	14.2	6.0	5.9
K1G5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	87	x	-	-	-	87	8700.0	1.0	-
K1P2	-	-	-	-	-	-	-	-	-	-	-	-	37	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	37	3700.0	1.0	-
K1G4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	64	x	-	-	-	64	6400.0	1.0	-
K1G3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	115	x	-	-	-	115	5700.0	1.0	1.0
K1P1	-	-	-	-	-	-	-	-	-	-	-	-	98	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	98	4800.0	1.0	-
K1G2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	54	-	-	-	-	54	5400.0	1.0	-
K1G1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	83	x	-	-	-	83	8300.0	1.0	-
K1	-	-	-	-	-	10	-	-	-	-	-	-	111	-	-	-	-	-	-	-	-	-	9	38	-	150	x	-	-	-	318	13.3	5.0	5.0

Raw Data - Knighton

	C.implicata	dalmanellids indet.	D.navicula	H.elegans	L.lata	M.nucula	P.minimus	S.ludloviensis	S.wilsoni	C.cornucopiae	P.tenuistriata	D.myops	beyrichiaceans	smooth ostracods	Fistulipora sp.	vinculariiform trepostome	Ó.subundulatum	graptolites	B.bohemicus	S.varians	S.incipiens	S.c.semispinosus	crinoid ossicles (round)	NUMBER OF INDIVIDUALS	DENSITY PER 5000 cm^3	NUMBER OF SPECIES	DIVERSITY PER 100 INDIV.
N6G2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	38	-	-	-	-	-	38	3800.0	1	-
N6P1	-	-	-	-	-	-	-	-	-	-	22	-	-	-	-	-	-	-	-	-	-	-	-	22	2200.0	1	-
N6G1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	27	-	x	x	x	-	27	2700.0	3	-
N6	-	-	-	-	-	-	-	-	-	2	21	-	-	-	-	-	2	22	-	x	x	x	-	47	2.0	4	-
N5P1	-	-	-	-	-	-	-	-	-	-	28	-	-	-	-	-	-	-	-	-	-	-	-	28	2800.0	1	-
NTH	-	25	3	-	-	42	-	-	2	-	-	-	-	-	3	-	-	-	-	-	-	-	1	76	9500.0	1	-
N5	-	-	-	-	-	-	-	-	-	2	21	-	-	-	-	-	3	10	-	-	-	-	-	36	1.5	4	-
NTG	-	11	5	1	-	82	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	1	104	13000.0	7	7.0
NTF	-	55	6	1	-	29	-	15	4	-	-	2	-	-	1	-	-	-	-	-	-	-	1	114	14250.0	9	8.8
N4P2	-	-	-	-	-	-	-	-	-	-	32	-	-	-	-	-	-	-	-	-	-	-	-	32	3200.0	1	-
NTE	3	8	19	-	-	30	-	4	10	-	-	-	4	-	3	1	-	-	-	-	-	-	1	83	10375.0	10	-
N4P1	-	-	-	-	-	-	-	-	-	-	28	-	-	-	-	-	-	-	-	-	-	-	-	28	2800.0	1	-
N4	-	-	-	-	1	-	-	-	-	5	32	-	-	-	-	-	4	13	x	-	-	-	-	55	2.3	5	-
N3P3	-	-	-	-	-	-	-	-	-	-	24	-	-	-	-	-	-	-	-	-	-	-	-	24	2400.0	1	-
N3P2	-	-	-	-	-	-	-	-	-	-	28	-	-	-	-	-	-	-	-	-	-	-	-	28	2800.0	1	-
NTD	1	7	6	3	-	28	-	5	12	-	-	-	-	-	2	2	-	-	-	-	-	-	1	67	8375.0	10	-
N3P1	-	-	-	-	-	-	-	-	-	-	32	-	-	-	-	-	-	-	-	-	-	-	-	32	3200.0	1	-
N3	-	-	-	-	3	-	-	-	-	6	22	-	-	-	-	-	8	9	x	-	-	-	-	48	2.0	5	-
NTC	-	8	16	-	-	13	-	2	-	-	-	-	-	-	3	2	-	-	-	-	-	-	1	45	5625.0	7	-
N2	-	-	-	-	-	-	-	-	-	-	23	-	-	-	-	-	5	9	-	-	-	-	-	37	1.5	3	-
NTB	-	19	9	-	-	9	1	3	2	-	-	-	-	-	3	-	-	-	-	-	-	-	1	47	5875.0	8	-
NTA	-	24	14	-	-	4	-	6	-	-	-	-	3	2	1	4	-	-	-	-	-	-	1	59	7375.0	9	-
N1	-	-	-	-	-	-	-	-	-	1	22	-	-	-	-	-	4	10	-	-	-	-	-	37	1.5	3	-

	A. grayi	C. implicata	dalmanellids indet.	D. navicula	H. elegans	L. lata	M. nucula	P. minimus	S. ludloviensis	S. wilsoni	S. euglypha	C. cornucopiae	C. planulata	L. reticulata	P. tenuistriata	beyrichiaceans	Fistulipora sp.	vinculariiform trepostome	'O'. subundulatum	graptolites	B. bohemicus	S. clunensis	crinoid ossicles (round)	NUMBER OF INDIVIDUALS	DENSITY PER 5000 cm^3	NUMBER OF SPECIES	DIVERSITY PER 100 INDIV.
D1P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	24	-	-	-	-	-	-	-	-	24	2400.0	1.0	-
D1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-	-	-	2	3	-	-	-	16	0.7	3.0	-
D2P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28	-	-	-	-	-	-	-	-	28	2800.0	1.0	-
D2P2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	89	-	-	-	-	-	-	-	-	89	5600.0	1.0	-
D2	-	-	-	-	-	-	-	-	-	-	-	2	-	-	30	-	-	-	4	9	-	-	-	45	1.9	4.0	-
DTA	-	-	3	21	1	-	23	-	9	35	-	3	-	-	-	-	1	-	-	-	-	-	1	97	12125.0	9.0	-
D3	-	-	-	-	-	-	-	-	-	-	-	1	-	-	18	-	-	-	2	5	-	-	-	26	2.2	4.0	-
D3P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	69	-	-	-	-	-	-	-	-	69	2900.0	1.0	-
D4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	23	-	-	-	2	6	-	-	-	31	1.3	3.0	-
D5P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	130	-	-	-	-	-	-	-	-	130	3600.0	1.0	-
D5	-	-	-	-	-	-	-	-	-	-	-	1	-	-	18	-	-	-	-	4	-	-	-	23	1.0	3.0	-
DTB	-	-	-	18	-	-	16	-	9	16	-	-	-	-	15	1	1	1	-	-	-	-	1	78	9750.0	9.0	-
D6P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	36	-	-	-	-	-	-	-	-	36	3600.0	1.0	-
DTC	-	-	3	15	-	-	27	-	4	41	-	1	-	-	7	-	1	-	-	-	-	-	1	99	12375.0	9.0	-
D6	-	-	-	-	-	1	-	-	-	-	-	-	-	-	21	-	-	-	1	6	-	-	-	29	1.2	4.0	-
DTD	-	-	6	13	-	-	44	-	7	8	-	-	-	-	-	-	1	-	-	-	-	-	1	80	10000.0	7.0	-
D7P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	26	-	-	-	-	-	-	-	-	26	2600.0	1.0	-
D7G1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	24	-	-	-	24	2400.0	1.0	-
D7	-	-	-	-	-	-	-	-	-	-	-	1	-	-	24	-	-	-	2	16	-	x	-	43	1.8	4.0	-
D8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15	-	-	-	-	3	-	-	-	18	0.8	2.0	-
DTE	-	2	6	24	-	-	17	-	34	17	-	-	-	-	-	-	-	-	-	-	-	-	1	101	12625.0	7.0	7.0
D9P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	-	-	-	-	-	-	-	-	14	2800.0	1.0	-
D9	-	-	-	-	-	-	-	-	-	-	-	1	-	-	22	-	-	-	-	9	-	-	-	32	1.3	3.0	-
DTF	-	-	8	10	-	-	41	2	3	7	-	-	2	1	-	-	-	-	-	-	-	-	1	75	9375.0	9.0	-
D10	-	-	-	-	-	-	-	-	-	-	-	2	-	-	17	-	-	-	4	5	-	-	-	28	1.2	4.0	-
D11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	16	-	-	-	3	4	-	-	-	23	1.0	3.0	-
DTG	2	-	5	28	-	-	47	-	8	12	-	-	-	-	-	-	3	-	-	-	-	-	1	106	13250.0	8.0	7.9
D12P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28	-	-	-	-	-	-	-	-	28	2800.0	1.0	-
D12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	1	3	-	-	-	12	0.5	3.0	-
D13P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	-	-	-	-	-	-	-	-	14	2800.0	1.0	-
DTJ	-	-	-	-	-	-	-	-	-	-	-	5	-	-	67	-	-	-	-	-	-	-	-	72	9000.0	2.0	-
D13	-	-	-	-	-	-	-	-	-	-	-	2	-	-	11	-	-	-	2	6	-	-	-	21	0.9	4.0	-
D14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-	2	-	-	-	10	0.4	2.0	-
DTH	-	-	10	15	-	-	121	-	3	58	-	-	-	-	3	-	4	-	-	-	-	-	1	215	13375.0	8.0	7.5
D15P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18	-	-	-	-	-	-	-	-	18	1800.0	1.0	-
DTI	2	2	7	15	2	-	27	-	-	44	3	1	-	-	4	-	-	1	-	-	-	-	1	109	13625.0	12.0	11.7
D15	-	-	-	-	-	-	-	-	-	-	-	1	-	-	13	-	-	-	2	6	x	-	-	22	0.9	4.0	-
D16	-	-	-	-	-	-	-	-	-	-	-	1	-	-	11	-	-	-	-	4	-	-	-	16	0.7	3.0	-
D17P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	46	-	-	-	-	-	-	-	-	26	2600.0	1.0	-
D17G1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	-	-	-	14	2800.0	1.0	-
D17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	-	-	-	1	4	-	-	-	19	0.8	3.0	-
D18P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	76	-	-	-	-	-	-	-	-	76	3800.0	1.0	-
D18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13	-	-	-	2	6	-	-	-	21	0.9	3.0	-

Raw Data - Kerry

	A. reticularis	D. navicula	H. elegans	H. canalis	I. orbicularis	L. lata	M. nucula	P. minimus	S. ludloviensis	S. wilsoni	indet. brachiopod	C. cornucopiae	C. subplanulata	P. tenuistriata	Proetus sp.	Fistulipora sp.	'O'. dimidiatum	'O'. subundulatum	P. ibex	graptolites	B. bohemicus	S. chimaera s.l.	crinoid ossicles (round)	NUMBER OF INDIVIDUALS	DENSITY PER 5000 cm^2	NUMBER OF SPECIES
B29	-	8	-	-	-	4	3	-	-	14	2	-	-	18	-	-	-	3	-	-	-	-	-	52	8.7	7.0
B28P1	-	-	-	-	-	-	-	-	-	-	-	-	-	78	-	-	-	-	-	-	-	-	-	78	3700.0	1.0
B28S1	-	11	-	-	-	-	1	-	-	12	-	-	-	-	-	-	-	-	-	-	-	-	-	24	2400.0	3.0
B28	-	7	-	-	-	2	3	-	-	12	1	-	-	11	-	-	-	4	1	-	-	-	-	41	6.8	8.0
B27S1	-	6	-	1	1	-	1	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	1	14	1400.0	6.0
B27	-	11	-	-	-	2	2	-	-	13	3	-	-	-	-	-	-	3	-	-	-	-	-	34	5.7	6.0
B26	-	11	-	1	-	1	2	-	-	11	-	-	-	-	-	-	-	3	-	-	-	-	-	29	4.8	6.0
B25S1	-	22	1	-	-	-	-	-	1	9	-	-	-	-	-	1	-	-	-	-	-	-	-	34	3400.0	5.0
B25	-	15	-	-	-	2	3	-	-	14	1	-	-	2	-	-	-	-	-	-	-	-	-	37	6.2	6.0
B24S2	-	26	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	29	2900.0	2.0
B24S1	-	9	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	12	1200.0	4.0
B24	-	29	-	-	-	3	4	-	-	26	-	-	-	-	-	-	-	3	-	-	-	-	-	65	10.8	5.0
B23	-	4	-	-	-	1	1	-	-	4	-	-	-	-	-	-	-	1	-	-	-	-	-	11	1.8	5.0
B22	-	6	-	-	-	1	1	-	-	6	-	-	-	-	-	-	-	1	-	-	-	-	-	15	2.5	5.0
B21	-	4	-	-	-	1	-	-	-	4	-	-	-	-	-	-	-	-	-	2	-	x	-	11	1.8	4.0
B20	-	6	-	-	-	1	1	-	-	3	-	-	-	3	-	-	-	-	-	-	-	-	-	14	2.3	5.0
B19	-	-	-	-	-	3	4	-	-	5	-	-	-	33	-	-	-	2	-	1	-	-	-	48	2.0	6.0
B18	-	5	-	-	3	-	3	1	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	19	3.2	5.0
B17P3	-	-	-	-	-	-	-	-	-	-	-	-	-	36	-	-	-	-	-	-	-	-	-	36	3600.0	1.0
B17P2	-	-	-	-	-	-	-	-	-	-	-	-	-	170	-	-	-	-	-	-	-	-	-	170	3800.0	1.0
B17P1	-	-	-	-	-	-	-	-	-	-	-	-	-	23	-	-	-	-	-	-	-	-	-	23	2300.0	1.0
B17	-	-	-	-	-	3	-	-	-	11	-	1	-	27	-	-	-	3	-	4	-	-	-	49	2.0	6.0
B16	1	8	3	1	4	-	2	-	-	14	-	-	-	-	1	-	-	-	-	-	-	-	1	35	5.8	9.0
B15P2	-	-	-	-	-	-	-	-	-	-	-	-	-	27	-	-	-	-	-	-	-	-	-	27	2700.0	1.0
B15P1	-	-	-	-	-	-	-	-	-	-	-	-	-	58	-	-	-	-	-	-	-	-	-	58	5800.0	1.0
B15	-	-	-	-	-	5	-	3	-	-	-	1	-	30	-	-	1	-	-	5	-	x	-	45	1.9	6.0
B14	-	-	-	-	-	3	1	-	-	6	-	1	-	28	-	-	2	4	-	-	-	-	-	45	1.9	7.0
B13	-	5	-	1	-	-	3	-	-	9	-	-	2	7	-	-	-	-	-	-	-	-	-	27	4.5	6.0
B12	-	-	-	-	-	3	1	-	-	1	-	2	-	24	-	-	-	2	-	-	-	-	-	33	1.4	6.0
B11	-	-	-	-	-	-	2	-	-	-	-	-	1	21	-	-	2	-	-	-	-	-	-	26	4.3	4.0
B10P3	-	-	-	-	-	-	-	-	-	-	-	-	-	46	-	-	-	-	-	-	-	-	-	46	2600.0	1.0
B10P2	-	-	-	-	-	-	-	-	-	-	-	-	-	78	-	-	-	-	-	-	-	-	-	78	2900.0	1.0
B10P1	-	-	-	-	-	-	-	-	-	-	-	-	-	23	-	-	-	-	-	-	-	-	-	23	2300.0	1.0
B10	-	-	-	-	-	3	-	-	-	2	-	1	-	40	-	-	1	-	-	1	-	x	-	48	2.0	6.0
B9	-	-	-	-	-	2	-	-	-	4	-	-	-	16	-	-	-	1	-	2	-	-	-	25	1.0	5.0
B8	-	-	-	-	-	3	-	-	-	2	-	1	-	18	-	-	-	1	-	2	-	-	-	27	1.1	6.0
B7	-	-	-	-	-	3	-	-	-	-	-	1	-	15	-	-	-	2	-	2	x	-	-	23	1.0	5.0
B6P1	-	-	-	-	-	-	-	-	-	-	-	-	-	302	-	-	-	-	-	-	-	-	-	302	2300.0	1.0
B6	-	-	-	-	-	3	-	-	-	5	-	2	-	19	-	-	-	2	-	4	-	-	-	35	1.5	6.0
B5P1	-	-	-	-	-	-	-	-	-	-	-	-	-	38	-	-	-	-	-	-	-	-	-	38	3800.0	1.0
B5	-	-	-	-	-	4	2	-	-	8	-	2	-	20	-	-	-	2	-	5	-	-	-	43	1.8	7.0
B4P2	-	-	-	-	-	-	-	-	-	-	-	-	-	24	-	-	-	-	-	-	-	-	-	24	2400.0	1.0
B4P1	-	-	-	-	-	-	-	-	-	-	-	-	-	28	-	-	-	-	-	-	-	-	-	28	2800.0	1.0
B4	-	-	-	-	-	3	-	-	-	1	-	-	-	24	-	-	-	-	-	6	-	-	-	34	1.4	4.0
B3	1	6	1	-	-	-	6	-	-	24	-	-	1	4	-	-	-	-	-	-	-	-	-	43	7.2	7.0
B2	-	-	-	-	-	-	-	-	-	-	-	1	-	40	-	-	-	2	-	-	-	-	-	49	2.0	3.0
B1	-	5	-	-	-	-	1	-	-	17	-	-	1	3	-	-	-	-	-	-	-	-	-	27	4.5	5.0

Raw Data - Builth Wells

	dalmanellids indet.	D. navicula	H. elegans	H. canalis	I. orbicularis	L. lata	M. cf. lepisma	M. nucula	O. rugata	P. minimus	S. ludloviensis	S. wilsoni	bivalve sp. C	C. cornucopiae	C. planulata	P. tenuistriata	beyrichieceans	encrusting trepostome	vinculariiform trepostome	Favosites sp.	'O'.dimidiatum	'O'.subumbulatum	P. ibex	graptolites	P. tumescens	S. chimaera s.l.	crinoid ossicles (round)	NUMBER OF INDIVIDUALS	DENSITY PER 5000 cm^3	NUMBER OF SPECIES
C53S2	-	7	-	-	-	-	-	1	-	-	-	5	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	13	2600.0	3.0
C53S1	-	6	-	-	-	-	-	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	1800.0	3.0
C53	-	19	-	1	-	1	-	2	-	-	-	8	-	1	-	-	-	-	-	-	-	2	1	-	-	-	-	35	5.8	8.0
C52	-	13	-	-	-	1	-	3	1	1	-	4	-	2	-	-	-	-	-	-	-	1	-	-	-	-	-	26	4.3	8.0
C51S1	-	14	-	-	-	-	-	9	-	-	-	7	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	31	3100.0	4.0
C51	-	17	-	1	1	2	-	2	-	-	-	12	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	36	6.0	7.0
C50S1	-	13	-	-	-	2	-	2	-	-	-	8	-	-	-	-	1	1	1	-	-	-	-	-	-	-	1	29	2900.0	8.0
C50	-	27	-	-	-	2	-	4	-	-	1	14	-	2	1	-	-	-	-	-	-	-	-	-	-	-	1	51	8.5	7.0
C49S1	-	23	-	-	-	1	-	7	-	-	-	2	-	-	-	1	-	-	-	-	-	-	1	-	-	-	1	36	3600.0	7.0
C49	-	15	-	1	-	2	-	3	-	-	-	4	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	27	4.5	7.0
C48S1	-	56	3	-	-	-	1	8	-	-	2	3	-	-	-	-	8	-	3	-	-	-	-	-	-	-	1	85	8500.0	9.0
C48	-	42	1	1	-	2	-	-	-	-	-	16	-	1	-	-	-	-	-	-	-	1	1	-	-	-	-	65	10.8	8.0
C47	-	15	-	1	-	4	-	1	-	-	-	7	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	30	5.0	7.0
C46	-	23	-	2	-	3	-	2	2	-	-	9	-	1	-	3	-	-	-	-	-	-	-	-	-	-	-	45	7.5	8.0
C45	-	23	-	1	1	3	-	4	1	-	-	19	1	1	-	-	-	-	-	-	-	-	1	3	-	-	-	58	9.7	11.0
C44S1	-	17	-	-	-	2	-	6	3	-	-	3	-	-	-	11	-	-	-	-	-	-	-	8	-	-	-	50	5000.0	7.0
C44	-	17	-	3	-	2	-	4	1	-	-	11	-	1	-	1	-	-	-	-	-	-	1	-	-	-	-	41	6.8	9.0
C43S1	-	7	-	-	-	3	-	-	1	-	-	1	-	5	-	14	-	-	-	-	-	-	-	-	-	-	1	32	3200.0	7.0
C43	-	16	-	1	-	3	-	2	2	-	-	9	-	4	-	5	-	-	-	-	-	1	-	1	-	-	-	44	7.3	10.0
C42	-	9	-	1	-	3	-	1	-	-	-	6	-	1	-	6	-	-	-	-	-	-	-	-	-	-	-	27	4.5	7.0
C41P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	82	-	-	-	-	-	-	-	-	-	-	-	82	2800.0	1.0
C41	-	5	-	1	-	2	-	2	-	-	-	8	-	1	-	13	-	-	-	-	-	3	-	-	-	-	-	35	5.8	8.0
C40P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	23	-	-	-	-	-	-	-	-	-	-	-	23	2300.0	1.0
C40	-	14	-	1	-	2	-	1	-	-	-	5	-	2	-	8	-	-	-	-	-	1	-	-	-	-	-	34	5.7	8.0
C39S2	4	42	-	1	8	-	-	4	-	-	1	4	-	-	-	4	-	-	-	-	-	1	-	-	-	-	-	69	6900.0	9.0
C39S1	-	13	-	-	-	11	-	4	-	-	-	13	-	-	-	8	-	-	-	-	-	-	-	-	-	-	-	49	4900.0	5.0
C39	-	11	-	2	-	7	-	5	1	-	-	15	3	2	-	5	-	-	-	-	-	1	-	1	-	-	-	53	8.8	11.0
C38S1	-	2	-	-	-	4	-	-	-	-	-	2	-	-	-	27	-	-	-	-	-	-	-	1	-	-	-	36	3600.0	5.0
C38	-	9	-	2	1	3	-	1	-	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	19	3.2	7.0
C37P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21	-	-	-	-	-	-	-	-	-	-	-	21	2100.0	1.0
C37	-	8	-	-	1	3	-	5	-	-	-	2	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	25	4.2	6.0
C36	-	8	-	-	2	3	-	2	-	2	-	1	-	2	-	10	-	-	-	-	-	-	-	-	-	-	-	30	5.0	8.0
C35P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	46	-	-	-	-	-	-	-	-	-	-	-	46	2800.0	1.0
C35	-	7	-	-	1	4	-	2	-	-	-	1	-	-	-	8	-	-	-	-	-	2	1	-	-	-	-	26	4.3	8.0
C34	1	4	-	1	-	2	-	1	-	-	-	1	-	2	-	5	-	-	-	-	-	1	-	-	-	-	-	18	3.0	9.0
C33	-	3	-	-	-	3	-	1	-	-	-	-	-	1	-	3	-	-	-	-	1	-	-	-	-	-	-	12	2.0	6.0
C32	-	3	-	-	-	2	-	-	-	-	-	2	-	1	-	5	-	-	-	-	-	2	-	-	-	-	-	15	2.5	6.0
C31P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	44	-	-	-	-	-	-	-	-	-	-	-	44	2200.0	1.0
C31	2	3	-	-	-	2	-	-	-	-	-	-	-	1	-	4	-	-	-	-	1	1	-	3	-	-	-	17	2.8	8.0
C30	-	2	-	-	-	2	-	-	-	-	-	1	-	1	-	4	-	-	-	-	-	-	-	1	-	-	-	11	1.8	6.0
C29	-	3	-	-	-	2	-	-	-	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	8	1.3	4.0
C28	-	1	-	-	-	2	-	1	-	-	-	1	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	9	1.5	5.0
C27	1	1	-	-	-	2	-	-	-	-	-	-	-	1	-	4	-	-	-	-	-	-	-	-	-	-	-	9	1.5	5.0
C26	-	1	-	-	-	3	-	-	-	-	-	-	-	-	-	14	-	-	-	-	-	-	-	-	-	-	-	18	3.0	3.0
C25P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	34	-	-	-	-	-	-	-	-	-	-	-	34	1700.0	1.0
C25	-	-	-	-	-	1	-	-	-	-	-	1	-	1	-	43	-	-	-	-	-	-	-	-	-	-	-	46	1.9	4.0
C24	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	27	-	-	-	-	-	-	-	1	-	-	-	31	1.3	3.0
C23P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28	-	-	-	-	-	-	-	-	-	-	-	28	2800.0	1.0
C23	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	38	-	-	-	-	-	-	-	1	-	-	-	42	1.8	3.0
C22P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	108	-	-	-	-	-	-	-	-	-	-	-	108	2200.0	1.0
C22	-	-	-	-	-	3	-	1	-	-	-	-	-	-	-	45	-	-	-	-	1	1	-	1	-	-	-	52	2.2	6.0
C21	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	32	-	-	-	-	-	-	-	3	-	x	-	37	1.5	3.0
C20P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	98	-	-	-	-	-	-	-	-	-	-	-	98	3600.0	1.0
C20	-	-	-	-	-	3	-	2	-	-	-	-	-	-	-	40	-	-	-	-	1	1	-	2	-	x	-	49	2.0	6.0
C19P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28	-	-	-	-	-	-	-	-	-	-	-	28	2800.0	1.0
C19	-	-	-	-	-	2	-	1	-	-	-	1	-	-	-	75	-	-	-	-	-	-	-	2	-	-	-	81	3.4	5.0
C18P2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	26	-	-	-	-	-	-	-	-	-	-	-	26	2600.0	1.0
C18P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	168	-	-	-	-	-	-	-	-	-	-	-	168	4600.0	1.0
C18	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	67	-	-	-	-	-	-	-	1	-	-	-	71	3.0	3.0
C17	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	23	-	-	-	-	1	-	-	-	-	-	-	27	1.1	3.0
C16	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	26	-	-	-	-	-	2	-	-	-	-	-	30	1.3	3.0
C15	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	21	-	-	-	-	-	-	-	-	-	-	-	24	1.0	2.0
C14	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	23	-	-	-	-	-	-	-	-	-	-	-	26	1.1	2.0
C13P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	48	-	-	-	-	-	-	-	-	-	-	-	48	1800.0	1.0
C13	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	27	-	-	-	-	-	-	-	-	-	-	-	29	1.2	2.0
C12P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	22	-	-	-	-	-	-	-	-	-	-	-	22	2200.0	1.0
C12	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	35	-	-	-	-	-	-	-	4	-	x	-	42	1.8	3.0
C11	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	11	-	-	-	-	-	-	-	-	-	-	-	13	0.5	2.0
C10P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	23	-	-	-	-	-	-	-	-	-	-	-	23	2300.0	1.0
C10	-	-	-	-	-	2	-	1	-	-	-	-	-	-	-	23	-	-	-	-	-	-	-	-	-	-	-	26	1.1	3.0
C9P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	22	-	-	-	-	-	-	-	-	-	-	-	22	2200.0	1.0
C9	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	31	-	-	-	-	-	-	-	1	x	-	-	35	1.5	3.0
C8P2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	20	2000.0	1.0
C8P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21	-	-	-	-	-	-	-	-	-	-	-	21	2100.0	1.0
C8	-	-	-	-	-	2	-	1	-	-	-	-	-	-	-	28	-	-	-	-	-	1	-	-	-	-	-	32	1.3	4.0
C7P2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	44	-	-	-	-	-	-	-	-	-	-	-	44	2200.0	1.0
C7P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25	-	-	-	-	-	-	-	-	-	-	-	25	2500.0	1.0
C7	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	41	-	-	-	-	-	-	-	-	-	-	-	43	1.8	3.0
C6P1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	38	-	-	-	-	-	-	-	-	-	-	-	38	1900.0	1.0
C6	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	35	-	-	-	-	-	-	-	1	x	-	-	37	1.5	3.0

Raw Data - Cwm Graig Ddu

Raw Data - Gwyddelfa

	A. reticularis	H. elegans	I. clivosa	I. orbicularis	L. depressa	L. filosa	M. cf. lepisma	M. nucula	S. wilsoni	S. euglypha	D. myops	smooth ostracods	Fistulipora sp.	P. lanceolata	vinculariiform trepostome	T. ornatus	Tentaculites sp.	crinoid ossicles (round)	NUMBER OF INDIVIDUALS	DENSITY PER 5000 cm^3	NUMBER OF SPECIES	DIVERSITY PER 100 INDIV.
G14	1	-	1	86	-	2	-	13	13	-	-	-	-	-	-	-	-	1	117	19.6	7.0	6.7
G13	-	-	1	70	-	6	-	14	10	-	-	-	-	-	-	-	1	1	103	17.2	7.0	7.0
GS7	70	-	-	15	-	10	-	-	4	-	-	-	-	-	4	-	-	1	104	815.2	6.0	6.0
G12	75	1	-	14	3	5	-	3	5	1	-	-	2	-	2	-	-	1	112	37.4	11.0	10.7
G11	11	2	-	66	1	4	-	2	13	-	2	-	-	-	4	-	-	1	106	35.4	10.0	9.9
GS6	68	-	-	33	-	2	-	-	4	-	-	-	-	-	-	-	-	1	108	780.5	5.0	4.9
G10	15	5	-	40	1	1	-	6	28	-	-	-	3	-	5	-	-	1	105	35.0	10.0	10.0
GS5	15	-	-	70	-	11	-	-	14	-	-	-	-	-	-	-	-	1	111	710.4	5.0	4.9
G9	21	1	-	65	11	9	-	2	6	-	1	-	1	-	1	-	-	1	119	39.6	11.0	10.0
G8	13	1	-	71	3	2	-	2	6	-	-	-	-	-	2	-	-	1	101	33.6	9.0	9.0
GS4	67	-	-	38	-	26	-	-	-	-	-	-	-	-	-	-	-	1	132	826.3	4.0	3.8
G7	103	-	-	21	3	3	-	2	4	-	-	-	3	1	4	-	-	1	145	58.8	10.0	9.4
G6	16	1	-	71	3	15	-	-	4	1	1	-	3	-	2	-	-	1	118	39.4	11.0	10.2
GS3	15	-	-	36	-	52	-	-	-	-	-	-	-	-	-	-	-	1	104	650.0	4.0	4.0
G5	17	-	-	41	1	51	-	-	-	-	-	-	1	1	3	-	-	1	116	61.0	8.0	7.6
G4	32	2	1	61	2	17	-	1	2	-	-	-	-	-	7	-	-	1	126	42.0	10.0	9.4
GS2	69	-	-	19	2	-	-	-	-	-	-	-	-	-	11	-	-	1	102	680.0	5.0	5.0
G3	58	-	-	27	4	7	-	-	2	3	-	-	-	-	7	-	-	1	109	37.0	8.0	7.9
GS1	81	-	-	19	2	-	-	-	-	5	-	-	3	-	10	-	-	1	121	806.7	7.0	6.8
G2	120	1	-	27	7	39	1	-	8	4	1	-	3	-	11	-	-	1	223	75.6	12.0	9.6
G1	24	-	-	60	3	1	-	-	3	1	-	1	-	1	5	1	-	1	101	33.6	11.0	11.0

Raw Data - Saddle

	A. reticularis	dalmanellids indet.	H. elegans	I. orbicularis	L. depressa	L. filosa	M. nucula	P. ludloviensis	S. lunata	S. wilsoni	Grammysia sp. A	Modiolopsis sp.	N. antiquus	Pteronitella sp.	Sanguinolites sp.	bivalve indet.	acastomorph trilobite	D. myops	smooth ostracods	Fistulipora sp.	vinculariiform trepostome	L. obsoletum	M. bullatum	crinoid ossicles (round)	crinoid ossicles (pentagonal)	NUMBER OF INDIVIDUALS	DENSITY PER 5000 cm^3	NUMBER OF SPECIES	DIVERSITY PER 100 INDIV.
SS19	-	-	-	-	-	-	10	49	-	-	8	4	-	34	-	43	-	-	-	-	-	-	-	-	-	148	50.0	6.0	6.0
SS18	-	13	2	-	-	-	5	10	126	4	-	-	-	4	-	3	-	-	-	-	2	-	-	1	1	171	4710.0	11.0	10.2
SS17	2	8	-	-	-	1	19	13	68	3	-	-	-	-	-	7	-	-	-	-	-	-	-	1	-	122	4525.0	9.0	8.6
SS16	-	6	1	-	-	-	31	45	107	8	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	199	4487.5	7.0	6.0
S10	-	-	-	-	-	-	2	4	1	-	-	-	-	8	-	1	-	-	-	-	-	-	-	-	-	16	3.0	5.0	-
SS15	-	14	16	-	-	86	58	28	160	46	-	-	-	1	-	1	-	-	-	-	-	-	-	1	-	411	4370.0	10.0	7.6
SS14	-	4	4	-	-	-	20	13	42	16	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	101	4010.0	8.0	8.0
S8	-	-	-	-	-	-	1	4	3	3	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	13	2.2	6.0	-
SS13	-	4	6	-	-	6	18	15	48	14	-	-	-	-	-	1	-	-	-	1	-	-	-	1	-	114	4140.0	10.0	9.7
SS12	2	10	7	-	-	4	30	55	125	41	-	-	2	-	-	-	-	-	-	-	-	-	-	1	-	277	4770.0	10.0	8.8
SS11	-	3	8	-	-	1	6	21	71	16	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	138	4380.0	9.0	8.1
S7	-	-	1	-	-	-	1	5	1	-	-	-	2	14	-	-	-	-	-	-	-	1	-	-	-	25	4.2	7.0	-
S6	-	-	2	-	-	-	1	3	2	8	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	17	2.8	6.0	-
SS10	-	5	10	-	-	59	50	27	77	51	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	280	4750.0	8.0	7.4
SS9	-	7	7	-	-	37	37	80	110	38	-	-	-	3	-	-	-	-	-	-	-	-	-	1	-	320	4000.0	9.0	8.2
S5	-	-	1	-	-	-	2	3	1	1	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-	15	2.5	6.0	-
SS8	2	2	-	-	-	-	22	21	45	42	-	-	-	1	-	3	-	-	-	-	-	-	-	1	-	139	4737.5	9.0	8.4
SS7	-	15	7	-	-	-	72	100	101	133	-	-	-	2	-	15	-	-	-	-	-	-	-	1	1	447	4793.8	10.0	7.8
SS6	1	12	7	-	-	6	17	139	138	79	-	-	-	3	-	-	-	-	-	-	-	-	-	1	-	403	4518.8	10.0	8.1
SS5	6	5	1	-	-	8	10	22	55	15	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	124	4033.3	10.0	9.4
SS4	28	13	1	-	1	33	76	88	156	91	-	-	-	7	-	-	-	-	-	-	-	-	-	1	-	495	4475.5	11.0	8.6
S4	-	-	-	-	-	-	-	7	23	15	-	3	2	4	-	-	-	-	-	-	-	-	-	1	-	55	9.2	7.0	-
S3	-	-	-	-	-	-	3	-	9	21	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	34	5.7	4.0	-
SS3	-	9	1	-	-	-	105	21	91	45	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	274	4826.7	8.0	6.2
SS2	2	12	9	1	-	1	57	4	90	8	-	-	-	6	1	-	2	-	-	-	1	-	-	1	1	196	4306.7	15.0	12.0
S2	-	-	1	-	-	1	12	2	27	4	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	49	8.2	8.0	-
SS1	5	2	1	-	-	-	15	7	32	4	-	-	-	11	-	2	-	1	-	-	-	2	-	1	-	83	4037.5	12.0	-
S1	-	-	1	-	-	-	2	2	18	4	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	29	4.8	7.0	-

Raw Data - Cennen

	A. reticularis	C. implicata	dalmanellids indet.	G. lata	H. elegans	I. cilyosa	I. orbicularis	I. deppressa	I. filosa	M. cf. lepisma	M. nucula	P. ludlowiensis	S. lumata	S. ludlowiensis	S. wilsoni	S. euglypha	G. cymbaeformis	Grammysia sp. A	L. reticulata	Pteronitella sp.	bivalves indet.	D. myops	homalonotid trilobite	Proetus sp.	beyrichiaceans	smooth ostracods	Fistulipora sp.	P. lanceolata	vinculariiform treposotome	L. obsoletum	solitary coral sp. B	T. ornatus	crinoid ossicles (round)	crinoid ossicles (pentagonal)	NUMBER OF INDIVIDUALS	DENSITY PER 5000 cm^3	NUMBER OF SPECIES	DIVERSITY PER 100 INDIV.
FS23	-	-	10	-	-	-	-	-	-	-	59	16	30	-	-	-	-	25	-	130	10	-	5	-	-	-	-	-	-	-	-	-	-	-	285	5346.2	8.0	8.0
FS22	-	-	8	-	-	-	-	-	-	-	85	27	51	-	-	-	3	21	-	238	8	-	4	-	-	-	-	-	-	-	-	-	-	-	450	4827.4	10.0	9.6
FS21	-	-	11	-	-	-	-	-	-	-	38	17	18	-	-	-	-	16	-	68	18	-	2	-	-	-	-	-	-	-	-	-	-	-	188	3872.1	8.0	8.0
FS20	-	-	8	-	-	-	7	-	1	-	18	6	68	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	2	-	-	112	4733.0	9.0	8.7
FS19	-	-	20	-	-	-	35	-	6	-	70	4	163	-	4	-	-	-	-	3	-	-	-	-	2	-	-	-	-	-	-	-	-	-	310	4428.6	10.0	9.6
FS18	-	-	11	-	-	1	8	-	-	-	22	3	62	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	107	4350.0	6.0	5.9
FS17	-	1	3	-	-	-	4	-	2	-	36	34	16	-	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	102	4400.0	10.0	10.0
FS16	-	-	9	-	1	-	7	-	5	-	24	33	30	-	1	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	118	3933.3	12.0	11.4
FS15	-	1	9	-	-	-	1	-	5	-	64	8	33	-	3	-	-	-	-	1	-	-	3	-	-	-	-	-	-	-	-	2	-	1	1	129	4300.0	11.0	10.2
F8	-	-	1	-	-	-	-	-	-	-	6	4	10	-	2	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	24	4.0	6.0	-
FS14	-	2	14	-	-	-	25	-	5	-	35	2	101	-	-	-	-	-	-	-	-	-	1	-	3	1	1	-	-	-	-	2	-	1	1	194	4850.0	15.0	12.5
FS13	-	-	13	-	-	-	28	-	-	-	47	4	76	-	-	-	-	-	-	-	1	-	-	-	2	-	1	1	-	-	-	2	-	1	1	174	4350.0	10.0	8.4
FS12	1	-	14	-	-	-	19	-	14	-	123	10	91	-	7	-	-	-	-	-	-	-	2	-	-	1	1	-	-	-	-	1	-	1	1	282	4700.0	11.0	8.6
F7	-	-	-	-	-	-	-	-	-	-	4	2	8	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	18	3.0	6.0	-
FS11	-	-	9	-	-	-	11	-	3	-	16	2	32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	75	3750.0	8.0	-
F6	-	-	1	-	-	-	-	-	1	-	10	4	9	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	1	28	4.5	7.0	-
FS10	-	-	11	-	-	-	18	-	34	-	53	35	78	-	3	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	1	235	3916.7	10.0	8.2
FS9	-	-	28	-	-	-	42	-	12	-	68	2	88	-	4	-	-	-	-	-	-	-	-	-	2	4	-	-	-	-	-	-	-	1	1	252	4200.0	11.0	9.4
F5	1	-	6	-	-	-	-	-	4	-	9	88	23	-	2	-	-	-	-	2	-	-	1	-	-	-	-	-	-	-	-	-	-	1	1	144	24.0	10.0	9.1
FS8	-	-	14	-	-	-	17	-	11	-	83	29	19	-	3	-	-	-	-	-	-	-	3	2	-	-	-	-	-	-	-	1	-	1	1	275	3928.6	12.0	9.9
F4	1	-	2	-	-	-	-	-	3	-	-	1	4	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	1	1	14	2.3	8.0	-
FS7	1	-	4	-	-	-	2	1	16	-	3	1	2	-	1	-	-	-	-	-	-	-	-	-	-	1	1	3	-	-	-	-	-	1	1	37	3850.0	13.0	-
FS6	-	9	19	1	-	-	31	-	21	16	74	-	26	-	23	-	-	-	-	-	-	-	-	-	-	-	-	1	-	27	-	-	-	1	1	249	3557.1	12.0	10.2
F3	3	-	1	-	-	-	9	-	-	-	4	1	6	-	5	-	-	-	-	2	-	-	-	-	-	-	-	1	-	1	-	2	-	1	1	16	2.7	6.0	-
FS5	-	-	10	2	-	-	10	-	7	1	31	1	6	-	7	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2	-	1	-	1	1	75	2500.0	13.0	-
FS4	-	-	11	-	-	-	10	-	7	1	31	-	5	-	7	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2	-	20	-	1	-	106	3533.3	11.0	10.8
FS3	-	10	18	-	-	-	18	-	12	-	25	3	11	-	4	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	102	3400.0	9.0	9.0
F2	2	-	5	-	-	-	-	-	1	-	-	-	4	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	16	4.4	6.0	-
FS2	-	-	19	1	-	-	27	-	7	1	17	3	16	-	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	102	3433.3	11.0	11.0
FS1	-	31	21	-	-	-	27	-	6	1	18	12	13	4	9	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	144	3600.0	12.0	11.1
F1	-	-	6	-	-	-	-	-	5	-	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	15	2.5	5.0	-

APPENDIX II

FAUNAL LIST

Faunal list of all the taxa identified during this work.

APPENDIX II

FAUNAL LIST

ANTHOZOA

Aulopora sp.
Favosites sp.
Lithostrotian sp.
Rhabdocyclus porpitoides (Lang & Smith)
small horn corals
solitary coral sp. A
solitary coral sp. B
Syringopora sp.

BRYOZOA

Ceramopora sp.
dendroid trepostome
encrusting cystoporate
encrusting trepostome
fenestelid bryozoan
Fistulipora sp.
Ptylodictya lanceolata (Goldfuss)
vinculariiform trepostome

BRACHIOPODA

Aegiria grayi (Davidson)
Amphistrophia funiculata (M'Coy)
Atrypa reticularis (Linnaeus)
Coolinia pecten (Linnaeus)
Craniops implicata (J. de C. Sowerby)
dalmanellids indet
small dalmanellid
Dayia navicula (J. de C. Swoerby)
Eospirifer radiatus (J. de C. Sowerby)
Gypidula galeata (Dalman)
Gypidula lata Alexander
Howellella elegans (Muir-Wood)
Hyattidina canalis (J. de C. Sowerby)
Isorthis clivosa Walmsley
Isorthis orbicularis (J. de C. Sowerby)

Kirkidium knightii (J. Sowerby)

Leptaena depressa (J. de C. Sowerby)

Leptostrophia filosa (J. de C. Sowerby)

Lingula lata J. de C. Sowerby

Lingula lewisii J. de C. Sowerby

Lingula sp. A

Mesopholidostrophia cf. lepisma (J. de C. Sowerby)

Microsphaeridiorhynchus nucula (J. de C. Sowerby)

Orbiculoidea rugata (J. de C. Sowerby)

Protochonetes ludloviensis Muir-Wood

Protochonetes minimus (J. de C. Sowerby)

Salopina lunata (J. de C. Sowerby)

Shagamella ludloviensis Boucot & Harper

Shaleria sp. nov.

indet. brachiopod

Sphaerirhynchia wilsoni (J. Sowerby)

Strophonella euglypha (Dalman)

BIVALVIA

Actinopteria pleuroptera (Conrad)

bivalve sp. A

bivalve sp. B

bivalve sp. C

bivalve indet.

Cardiola cornucopiae Goldfuss

Cypricardinia planulata (Conrad)

Cypricardinia subplanulata Reed

Goniophora cymbaeformis (J. de C. Sowerby)

Grammysia sp.

Grammysia sp. A

Limoptera reticulata (J. de C. Sowerby)

Modiolopsis sp.

Nuculites antiquus (J. de C. Sowerby)

Orthonota nasuta Conrad

? Paracyclus sp.

Plethomytilus mytilimeris (Conrad)

Praectenodonta ludensis (Reed)

Pterinea tenuistriata (M'Coy)

Pteronitella retroflexa (Wahlenberg)

Pteronitella sp.

Sanguinolites sp.

Tolmaia sowerbyi (M'Coy)

GASTROPODA

Bembexia lloydii (J. de C. Sowerby)

Bucanopsis sp.

Liospira striatissima (Salter)

Loxonema obsoletum (J. de C. Sowerby)

Poleumita globosa (Schlotheim)

Poleumita sp. nov.

CEPHALOPODA

'Cyrtoceras' sp.

Dawsonoceras nicholianum (Blake)

Gomphoceras sp.

Kionoceras angulatum (Wahlenberg)

Michelinoceras bullatum (J. de C. Sowerby)

'Orthoceras' dimidiatum (J. de C. Sowerby)

'Orthoceras' subundulatum Portlock

Paraphragmites ibex (J. de C. Sowerby)

TRILOBITA

acastomorph trilobite

Calymene sp.

Calymene cf. lawsoni Shirley

Dalmanites myops (König)

Encrinurus rosensteinae Tripp, Temple & Gass

Encrinurus stubblefieldi Tripp

Hemiarges sp.

homalonotid trilobite

Proetus astringens Owens

Proetus obconicus Lindström

Proetus sp.

OSTRACODA

beyrichiaceans

smooth ostracods

CRINOIDEA

crinoid columnals (round)

crinoid columnals (pentagonal)

GRAPTOLOIDEA

Bohemograptus bohemicus (Barrande)

Bohemograptus bohemicus cf. tenuis (Bouček)

graptolite indet.

Pristograptus tumescens (Wood)

Saetograptus chimaera (Barrande) s.l.

Saetograptus chimaera salweyi (Lapworth)

Saetograptus chimaera semispinosus (Elles & Wood)

Saetograptus clunensis (Earp)

Saetograptus incipiens (Wood)

Saetograptus varians (Wood)

Saetograptus varians subsp. nov.

MISCELLANEA

Cornulites serpularis Schlotheim

Keilorites sp.

Serpulites longissimus J. de C. Sowerby

Tentaculites ornatus J. de C. Sowerby

Tentaculites sp.

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